CLARK'S NUTCRACKERS AND WHITEBARK PINE:

RESILIENCE OF A KEYSTONE MUTUALISM IN AN ALTERED ECOSYSTEM

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In the face of widespread environmental change, understanding and promoting resilience and stability of plant-animal seed disperser mutualisms is key to effective conservation strategies. My two primary objectives were to (1) investigate the response of the keystone mutualism between whitebark pine (*Pinus albicaulis*) and Clark's nutcrackers (*Nucifraga columbiana*) to declining habitat in the Greater Yellowstone Ecosystem, and (2) suggest management strategies to help ensure persistence of Clark's nutcrackers, and their important seed dispersal function. Between 2009 and 2016, I studied Clark's nutcracker demography and behavioral plasticity by evaluating breeding ecology, space use, seasonal habitat selection and use, foraging ecology, and emigration, as a function of habitat quality and abundance. I carried out occupancy surveys, tracked individuals via radio and satellite, conducted behavioral observations, and monitored nests. Clark's nutcracker demography and behavior was intimately associated with whitebark pine habitat. Population-wide failure to breed followed low whitebark pine cone crops, and in breeding years, fledging success increased with whitebark pine abundance, but decreased in higher mortality stands. Clark's nutcracker occurrence was associated with both presence of cone-bearing whitebark pines, and landscape-scale abundance of the pines, suggesting conservation strategies should focus efforts at the landscape scale. The birds selected disproportionately high amounts of Douglas-fir (*Pseudotsuga menziesii*) habitat for their home

range, and foraged heavily on Douglas-fir cones, suggesting that whitebark pine should be managed within a habitat mosaic with Douglas-fir. The Clark's nutcracker-whitebark pine mutualism appears functional in the region because birds were available to disperse seeds. However, it is unclear whether the mutualism is stable. Clark's nutcrackers are highly mobile facultative migrants, and the majority of radio- and satellite-tagged birds disappeared during both the 2012 high and 2015 moderate whitebark pine cone crops. Managing Clark's nutcrackers presents a complex conservation challenge, but I suggest promoting stability of Clark's nutcracker populations, and focusing on the metapopulation in particular, is necessary for effective whitebark pine conservation. In this dissertation, I conclude by outlining recommended management strategies and key research questions that still need to be answered, finishing with important considerations that should be taken into account when designing a conservation plan for plant-animal seed disperser mutualisms.

BIOGRAPHICAL SKETCH

Taza Schaming grew up on a small farm in East Berne, NY, U.S.A. From an early age, she embraced every opportunity to spend her free time outdoors. Taza studied biology at Tufts University, and received a Bachelor of Science in 2001. During her time as an undergraduate, Taza worked in Dr. Meller's lab, studying gene expression in *Drosophila melanogaster*, and contributed to a graduate project, assessing terrestrial habitat requirements of the blue-spotted salamander (*Ambystomatidae laterale*), a species of special concern. She attended the School for International Training's biodiversity and conservation program in Tanzania, where she studied tree dominance in the montane rainforest of Mazumbai. After finishing her B.S., Taza lived, worked, and traveled around the world for six years. She worked for Point Reyes Bird Observatory in the sagebrush habitat of southeastern Wyoming, investigating the effects of natural gas development on avian survival and reproductive success, volunteered with Inti Wara Yassi, an animal rehabilitation center in Villa Tunari, Bolivia, and studied birds, vernal pools, and invasive species with the U.S. Fish and Wildlife Department in eastern Massachusetts. Following these experiences, she transitioned to working for Environmental Compliance Services (ECS), a private consulting company. While at ECS, she enrolled in her first graduate classes in environmental management at Harvard University. Taza has also spent three seasons backcountry snowboarding in the Rockies and Andes, learning difficult orienteering skills, and extreme self-reliance and independence. She spent a year in South America, climbing and snowboarding in remote mountains, volunteering, and exploring the diverse cultures and ecosystems of the Andes. She has also studied in Australia, trekked in Nepal, and travelled through Kenya, Malaysia, New Zealand, Canada and Cuba. Taza entered the M.S./PhD. program

at Cornell University in 2007, and completed her M.S. degree in May 2010. For her M.S. research, she studied seasonal variation in the onset of incubation, clutch size, and hatching failure in House Wrens (*Troglodytes aedon*) in Ithaca, NY. Since 2009, Taza has been studying a population of Clark's Nutcrackers (*Nucifraga columbiana*) in the Greater Yellowstone Ecosystem, with the ultimate goals of understanding impacts of habitat decline on mutualism breakdown, and designing biologically informed management interventions to help ensure persistence of Clark's nutcrackers. Taza is developing the Clark's nutcracker-whitebark pine (*Pinus albicaulis*) research as a long-term project. Along with her research, Taza married Pocholo Martinez in spring 2014. Suneva Schaming Martinez, their baby girl, was born April 2015. Taza is looking forward to raising Suneva with a pair of binoculars in her hand.

To Suneva Schaming Martinez.

Because of you, I am even more determined to make this world a better place.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION: CLARK'S NUTCRACKERS AND WHITEBARK PINE, A KEYSTONE MUTUALISM IN AN ALTERED ECOSYSTEM

Introduction

Habitat loss and degradation are increasingly common, and are considered severe threats to biodiversity because they are key drivers of global species loss [1,2]. When the conservation goal is to protect a species or to restore a degraded ecosystem, one of the essential requirements is to focus on integrity of the interactions, not just on individual species. Plant-animal seed disperser mutualisms in particular are critical to healthy ecosystem function in many communities [3–5]. These mutualisms can enhance ecosystem and species resilience in the face of habitat change by enabling colonization and regeneration of deforested, remote, and disturbed habitats [6–8]. Worldwide declines in animal seed dispersers [3,5,9] have increased the importance of determining how to promote mutualism stability and resilience, and hence prevent mutualism breakdown. My thesis tackles the question of how to analyze these interactions and how to manage for them at relevant scales.

Clark's nutcrackers (*Nucifraga columbiana*) are a keystone species in western North America: they are facultative mutualists of multiple conifers, playing an important role in forest regeneration and seed dispersal for at least ten conifer species [See 10]. Clark's nutcrackers shape the ecosystems in which they live. Annually, individuals are estimated to store between 32,000 and 98,000 seeds in thousands of separate locations [11,12]. Seeds not retrieved for food are able to germinate [11,12]. Clark's nutcrackers disperse seeds up to 32.6 km, effectively

moving seeds longer distances than wind, rodents and all other North American seed hoarding birds [13]. This dispersal enables rapid migration of seeds, contributes to gene flow across and between habitat islands, and moves seeds up in altitude and elevation, as well as into disturbed areas [13,14]. In the face of current climate change, the long-distance dispersal of conifer seeds, and thus the continued association between Clark's nutcrackers and conifers, may be critical in mitigating against local genetic bottlenecks and inbreeding depression, by bolstering effective population size, and facilitating rapid colonization of newly available ideal habitats [15].

The whitebark pine (*Pinus albicaulis*) is an obligate mutualist of the Clark's nutcracker because its seedlings sprout almost exclusively from Clark's nutcracker seed caches [11,16]. Whitebark pine is a critical component of treeline and subalpine ecosystems in western North America, contributing to biodiversity and performing multiple ecosystem services [14]. It is a keystone species in some communities because many animal species, including the grizzly bear (*Ursus arctos),* forage on its high-fat, high-energy nuts [14,17]. Whitebark pine is also valuable for watershed protection because it delays snowmelt, leading to decreases in both spring flooding and summer droughts [18,19].

Currently, whitebark pine forest communities are rapidly disappearing range-wide due to decades of fire suppression, widespread infection by the nonnative white pine blister rust (*Cronartium ribicola*), and outbreaks of mountain pine beetles (*Dendroctonus ponderosae*) [14,20]. These outbreaks have been worsened by favorable effects of global warming on bark beetle reproduction [21]. In a 2004-2006 study in the Northern Divide Ecosystem, nearly 75% of the whitebark pine were dead, and over 90% of the living trees were infected with blister rust [22]. Currently, 46% of the whitebark pine stands in the Greater Yellowstone, one of the healthiest remaining whitebark pine ecosystems, are classified as "high mortality" [23]. Due to

ongoing threats and heavy mortality, whitebark pine is a candidate for listing under the U.S. Endangered Species Act, and is listed as an endangered species in Canada [24,25]. This high whitebark pine mortality may seriously reduce biodiversity and disrupt many species interactions [26].

Although the Clark's nutcrackers eat seeds of multiple conifers [27], evidence from local studies suggests that whitebark pine declines have led to reduced local Clark's nutcracker populations [20,28,29]. Breeding bird survey results suggested a stable or increasing Clark's nutcracker population range-wide until the last several years [30]. Then, between 2006 and 2011, Clark's nutcracker populations declined in 54% of the states and provinces where they are found [30]. Clark's nutcrackers are facultative migrants, and in years with food shortages, the birds will move out of an ecosystem [31]. Although local populations may decline, it is unknown how the metapopulation is being affected by large-scale loss of the conifer habitats on which the birds depend. Clark's nutcrackers are still relatively common in the Greater Yellowstone Ecosystem [15]. However, no one has quantified how the decline of whitebark pines has impacted Clark's nutcracker demography and behavior in the region. Although Clark's nutcrackers use other food resources in the ecosystem, including limber pine (*Pinus flexilis*) and Douglas fir (*Pseudotsuga menziesii*), it is unlikely that these other resources are sufficient for maintaining Clark's nutcracker populations [15,32].

Clark's nutcrackers are poorly studied, in part due to their remote range [27,33]. Most previous Clark's nutcracker research has been restricted to observational studies on occupancy, harvesting, and caching behavior [14,29]. In addition, recent research reveals that conventional songbird survey methods – point counts, playback point counts, line transects, and distance sampling – do not reliably detect the birds, and the North American Breeding Bird Survey and

Christmas Bird Count do not dependably monitor resident Clark's nutcracker populations [27,34]. Only one systematic study of Clark's nutcracker habitat selection has been previously carried out, in the Cascade Range, Washington [10]. No-one has conducted research on Clark's nutcrackers on a spatial scale ecologically relevant to the space used by individual Clark's nutcrackers.

Understanding Clark's nutcracker demography and behavior in relation to habitat is pivotal to designing effective management plans for Clark's nutcracker and whitebark pine conservation. In addition, quantifying both the scale at which Clark nutcrackers track resources across the larger geographic landscape, and Clark nutcracker habitat suitability are necessary to understand the functional role of the birds in providing seed dispersal ecosystem services across the western landscape. Understanding the response of this keystone mutualism to a rapidly changing ecosystem both has immediate conservation implications, and advances our understanding of the impact of habitat degradation on mutualism stability and the persistence of forest community dynamics.

Since 2009, my two primary goals have been to (1) assess the impact of the decline of whitebark pine on Clark's nutcrackers and their functional role as conifer seed dispersers, and (2) suggest management strategies to help ensure persistence of Clark's nutcrackers and restore whitebark pine communities. Specifically, I investigated Clark's nutcracker demography and behavioral plasticity by evaluating breeding ecology, space use, seasonal habitat selection and use, foraging ecology, and emigration, as a function of habitat quality and abundance. With insights from this system, I address the fundamental question of how habitat loss and degradation affect mutualistic plant-animal disperser relationships, and discuss considerations that should be addressed when designing a conservation plan for these important mutualisms. In c*hapters 2 – 4,*

I primarily focus on breeding ecology, habitat selection and foraging ecology, and habitat use, respectively. *Chapter 5* is a synthesis of the insights that emerge from this body of research, including ideas based on both the earlier chapters and the unpublished results referred to below.

Understanding the impact of environmental variation on demographic variables is crucial to predicting how populations will respond to habitat loss. In *chapter 2*, I examine how population-wide breeding effort is associated with whitebark pine cone crop the previous fall, snowpack and temperature. My primary objective in the chapter is to evaluate conditions that may contribute to Clark's nutcrackers' population-wide failure to breed. In the process, I assess how adult prebreeding and breeding season body condition index varied between breeding and nonbreeding years. In *chapter 5*, I briefly discuss how reproductive success varies as a function of habitat in a breeding year.

Assessing both habitat selection and use allows for an optimal understanding of a species' relationship with habitat, because each illuminates different aspects of the relationship. First, in *chapter 3*, I evaluate Clark's nutcracker breeding season home range size, territoriality, and habitat selection in the southern Greater Yellowstone Ecosystem. I focus on the breeding season only because it is a critical stage of the birds' annual cycle, and we have little information on the habitats used by breeding birds [27,33]. An understanding of space use and habitat selection is particularly important during the breeding season, if managers want to ensure that a stable population of Clark's nutcrackers persists in an ecosystem. Additionally, it is necessary to understand variability in space use to predict how individuals will respond to habitat decline and changing environmental conditions. Therefore, I focused on comparing the home range and habitat selection of Clark's nutcrackers during two breeding seasons with extreme demographic and environmental differences, 2011, a population-wide nonbreeding year that followed a low

whitebark pine cone crop, and 2012, a breeding year that followed a high cone crop. In *chapter 5*, I expand beyond the breeding season, and briefly discuss the home range and habitat selection of radio- and satellite-tagged Clark's nutcrackers during the entire preharvest season, the time prior to the harvest of mature whitebark pine seeds (January through early August).

In *chapter 4*, to understand environmental drivers of Clark's nutcracker habitat use, I examine which habitat characteristics influenced Clark's nutcracker occurrence between 2009 and 2013. I focus on evaluating which scale of whitebark pine habitat the birds responded to – cone presence or density, local presence or abundance of the pines, or landscape scale abundance of the pines. Additionally, I assess how the birds were influenced by local or landscape-scale Douglas-fir habitat, the primary local alternative seed source. I examine how associations between habitat variables and occurrence changed over the year, by separately evaluating occurrence patterns during five stages of the annual cycle, breeding season, early summer, late summer, fall seed harvest and postharvest. In both *chapters 4 and 5*, I discuss how habitat selection and habitat use results complement each other.

Foraging is fundamental to an animal's survival and reproduction. Understanding how foraging behavior varies under different environmental conditions and in different habitats enables better predictions of how animals will respond to environmental change. In *chapter 3*, I examine Clark's nutcracker food types and foraging habitat selection during the breeding season. To evaluate the impact of whitebark pine cone crop on foraging the following spring, I focus on whether the breeding birds, in a year following a high whitebark pine cone crop, and nonbreeding birds, in a year following a low whitebark pine cone crop, varied in their foraging behavior. I specifically focused on the importance of cached seeds, which is widely considered to be a critical part of the diet, as well as use of different conifer seed types [35–37]. In *chapter 5*, I

briefly expand beyond the breeding season, and discuss Clark's nutcracker food types and foraging habitat selection over the preharvest season.

Continued residency, as well as emigration and immigration could all vary with landscape or patch quality, and therefore, habitat quality influences changes in distribution and population structure of both animal seed dispersers and dispersed tree species [38,39]. In *chapter 5*, I briefly discuss rates of emigration as well as the timing of the disappearance of radio- and satellite-tagged Clark's nutcrackers in relation to whitebark pine cone crop. I also discuss the Clark's nutcrackers' emigrant and resident strategies, and how these strategies may affect the future trajectory of the Clark's nutcracker metapopulation in the face of large-scale habitat decline [31].

One of my primary objectives was to suggest conservation strategies to help ensure persistence of Clark's nutcrackers and restore whitebark pine communities. In *chapters 2 – 4*, I suggest management strategies based on breeding ecology, habitat selection and habitat use results, respectively. In *chapter 4*, I also compare my occurrence results with the numbers predicted by previous models of Clark's nutcracker occurrence, and discuss the inconsistencies. I examine what we know, and what we still need to learn regarding the stability of the Clark's nutcracker mutualism in *chapter 4*, then expand the discussion in *chapter 5*.

Finally, *chapter 5* is a synthesis of the broader insights stemming from this body of research. I discuss how the culmination of what I have learned contributes to management strategies for Clark's nutcrackers and whitebark pine ecosystems. In addition, I outline future research questions we need to answer to properly manage the Clark's nutcracker-whitebark pine mutualism. Finally, I discuss what these results and insights mean for our understanding of plant-animal seed disperser mutualisms within the context of conservation. Promoting the resilience

and stability of plant-animal seed disperser mutualisms is critical to effective conservation in many ecosystems.

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CHAPTER 2

POPULATION-WIDE FAILURE TO BREED IN THE CLARK'S NUTCRACKER (*NUCIFRAGA COLUMBIANA*) [1]

Abstract

In highly variable environments, conditions can be so stressful in some years that entire populations forgo reproduction in favor of higher likelihood of surviving to breed in future years. In two out of five years, Clark's nutcrackers (*Nucifraga columbiana*) in the Greater Yellowstone Ecosystem exhibited population-wide failure to breed. Clark's nutcrackers at the study site experienced substantial interannual differences in food availability and weather conditions, and the two nonbreeding years corresponded with low whitebark pine (*Pinus albicaulis*) cone crops the previous autumn (≤ an average of 8 ± 2 cones per tree versus ≥ an average of 20 ± 2 cones per tree during breeding years) and high snowpack in early spring (≥ 61.2 ± 5.5 cm versus ≤ 51.9 ± 4.4 cm during breeding years). The average adult body condition index during the breeding season was significantly lower in 2011 (-1.5 ± 1.1), a nonbreeding year, as compared to 2012 (6.2 ± 2.0), a breeding year. The environmental cues available to the birds prior to breeding, specifically availability of cached whitebark pine seeds, may have allowed them to predict that breeding conditions would be poor, leading to the decision to skip breeding. Alternatively, the Clark's nutcrackers may have had such low body energy stores that they chose not to or were

[1] Schaming, T. D. 2015. Population-wide Failure to Breed in the Clark's Nutcracker (*Nucifraga columbiana*). PLOS ONE. 10(5): e0123917. doi:10.1371/journal.pone.0123917.

unable to breed. Breeding plasticity would allow Clark's nutcrackers to exploit an unpredictable environment. However, if large-scale mortality of whitebark pines is leading to an increase in the number of nonbreeding years, there could be serious population-level and ecosystem-wide consequences.

Introduction

The ability to modify reproduction as a function of environmental conditions better allows species to exploit variable, unpredictable environments [1,2]. Life-history theory suggests individuals should adopt a bet hedging strategy to maximize fitness in variable environments in which they reduce annual reproduction in poor years to increase survival and lifetime reproductive success [3,4]. Foregoing a breeding season may be an adaptive plastic response, favored when the value of immediate reproduction is low compared to the value of survival and future reproductive opportunities [5,6]. In highly variable environments, conditions can lead to such poor potential for breeding that all individuals in a population forgo reproduction in favor of higher likelihood of surviving to breed in future years. Although the proximate mechanisms remain poorly understood [7], population-wide failure to breed can come about in two non-mutually exclusive ways. First, if, prior to the onset of breeding, reliable cues are available indicating that environmental quality will adversely affect that year's reproductive success, individuals could use these cues to adaptively modify reproductive effort, potentially foregoing breeding all together [8,9]. Second, if prebreeding food supplies or weather are unfavorable, the entire population may have such low body energy stores as compared to body size that it is beneficial to skip a year before attempting to breed; this may either be an adaptation or a constraint [10,11].

Overall, conditions favoring population-wide failure to breed should be relatively

uncommon, occurring mainly in ecosystems with extreme annual variation in resources (e.g. food) and weather, such as arid systems or montane regions [12–14]. Montane areas are therefore ideal locations for investigating behavioral responses that permit or limit reproductive success in highly variable environments [15]. Previous research suggests that population-wide failure to breed is primarily correlated with low food availability or precipitation (drought, high rain or snow) which decreases food supplies [12–14].

With climate change, increased environmental disturbance, landscape change, and declining forest health, instances of failing to breed may become increasingly common and may represent a potential cause of population decline and local extinction. Habitat specialists in particular may be vulnerable to environmental change if they do not adapt. This places a premium on understanding the contexts and causes of the decision to forego breeding for populations under threat of becoming endangered or at risk of extinction.

The Clark's nutcracker is a long-lived, facultative partial migrant at high altitudes in the montane ecosystems of the western U.S. and Canada [16,17]. They specialize on seeds of masting conifer species, and rely on cached seeds for both overwinter survival and breeding [17,18]. They are unusual in that they primarily feed their young seeds cached the previous autumn [18]. Thus, they have unusually accurate information about spring food supplies at the time when they would initiate breeding. It is not clear how long Clark's nutcracker spatial memory of seed cache locations lasts. Field observations suggest Clark's nutcrackers remember the location of cache sites for seven to nine months [19]. Laboratory experiments showed that Clark's nutcrackers begin to forget the locations between 183 and 285 days [19]. After 285 days, many remaining seeds will have germinated, spoiled or been robbed by other animals, so it is unlikely caches would continue to be available for multiple years [19]. Therefore, caches from

333 years with high cone crops would not supplement the diet during low cone crop years. Clark's
334 nutcracker populations are highly sensitive to variation in the annual cone crop of conifers such
335 as whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*) and ponderosa pine (*P. ponderosa*);
336 they have been reported to irrupt during years of cone crop failure [20,21].

337 Ecosystems throughout the Clark's nutcracker range are currently under threat due to
338 decades of fire suppression, widespread infection of five-needled pines by the non-native fungal
339 pathogen *Cronartium ribicola*, which causes white pine blister rust, and outbreaks of mountain
340 pine beetles (*Dendroctonus ponderosae*) [22]. Despite the Clark's nutcrackers' capacity for wide
341 ranging movement, evidence suggests several populations are declining, including those in
342 "pristine" environments such as Glacier National Park in Montana and the Cascade Mountains of
343 Washington [23].

344 This study is based on five years of field work in the Greater Yellowstone Ecosystem. It
345 involved documenting population-wide breeding effort in a relatively robust population of
346 Clark's nutcrackers in a community where the whitebark pine trees they depend upon for food
347 are in decline [24]. Previously, all that was known of Clark's nutcracker breeding biology was
348 based on monitoring relatively few nests (n = 16 nests from two different studies [18,25]), and
349 few accounts of fledgling observations (e.g. [26,27]). Despite the low number of nests
350 monitored, some previous studies have suggested that Clark's nutcrackers may forego breeding
351 in years with low food [18,26].

352 Clark's nutcrackers are a keystone species in western North America because they play
353 an important role in forest regeneration and seed dispersal for at least ten conifer species (see
354 references within [28]). Whitebark pine, a keystone species and a candidate species under the
355 Endangered Species Act, is an obligate mutualist of Clark's nutcrackers because it germinates

almost exclusively from Clark's nutcracker seed caches [28–30]. Understanding causes of Clark's nutcracker failure to breed provides important information relevant to their conservation, as well as conservation of the fragile high elevation ecosystems they inhabit. These ecosystems provide essential services, including retention of snowpack critical for maintaining water supplies for much of the western U.S. [31]. My primary objective in this paper is to evaluate the conditions which may contribute to Clark's nutcrackers' population-wide failure to breed.

Methods

Ethics statement

I captured and handled all birds according to Animal Care Protocol guidelines approved by Cornell University. This research was approved by the Cornell University Institutional Animal Care and Use Committee (protocol # 2008-0176). I banded under U.S. Fish and Wildlife Permit # 23533, and Wyoming Game and Fish Chapter 33 Permit # 695. I conducted all field work under U.S. Forest Service Special-Use Authorization # JAC747002 (2009-2013) and Grand Teton National Park Scientific Research and Collecting Permit #'s GRTE-2011-SCI-0052 and GRTE-2012-SCI-0069.

Field methodology

Study site

I documented Clark's nutcracker breeding activity between 2009 and 2013 in the Greater Yellowstone Ecosystem, primarily in Bridger Teton and Shoshone National Forests, and Grand Teton National Park (25,050 km^2; bounded by 45º00'01" N north, 42º09'14" N south, 111º02'56"W west, and 108º42'55"W east; Fig. 2.1). The forested habitat primarily consists of whitebark pine, limber pine, Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus*

contorta), Engelmann spruce (*Picea englemannii*), and subalpine fir (*Abies lasiocarpa*), intermixed with sagebrush (*Artemesia tridentata*) - grass open areas, high mountain meadows and rocky outcroppings.

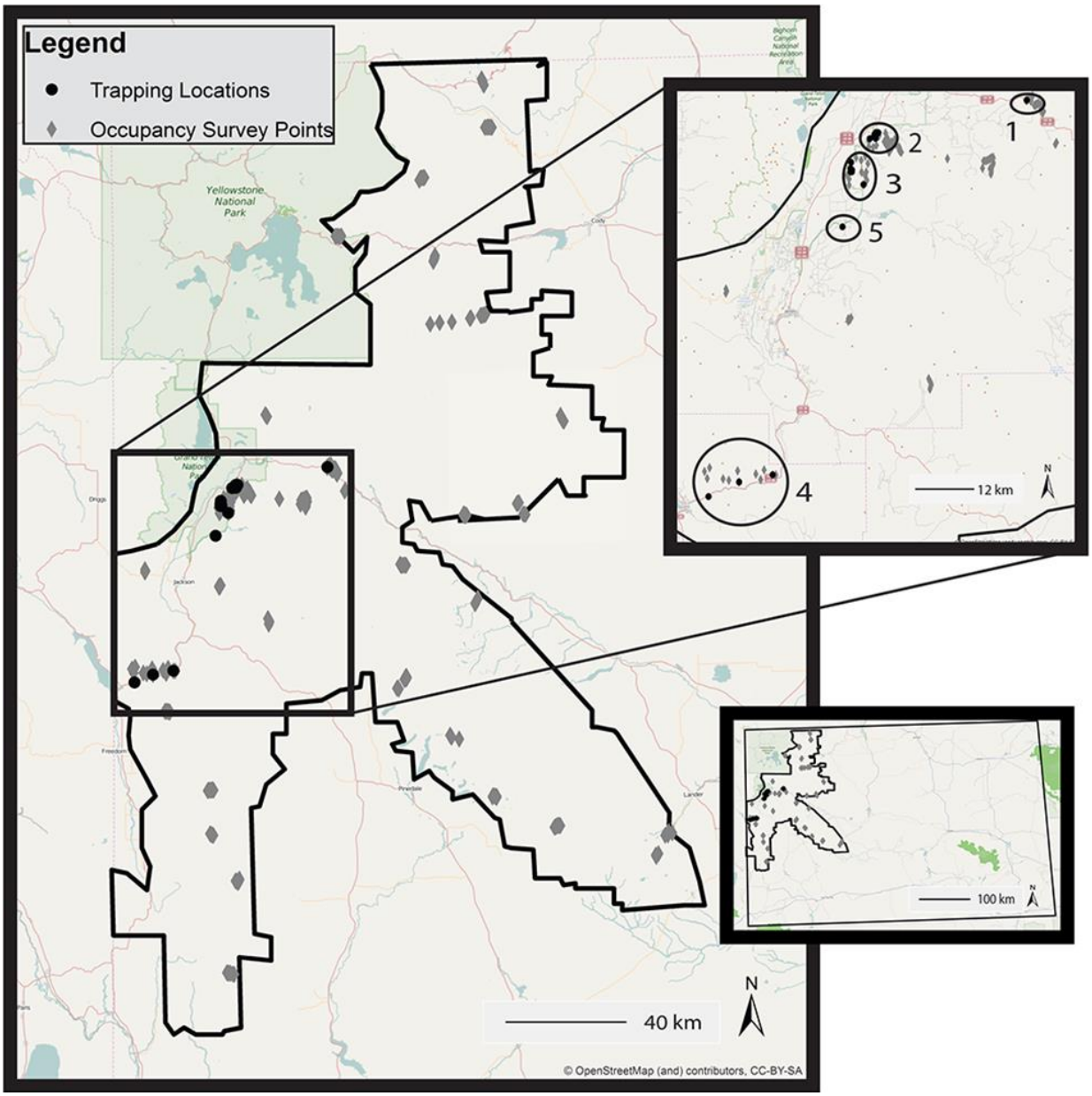

Figure 2.1. Study area in the Greater Yellowstone Ecosystem. The study area is outlined in black. I spent the majority of time in the field trapping and radio tracking Clark's nutcrackers, and hiking to and conducting occupancy surveys. The top inset map delineates the five trapping

385 locations. The bottom inset map depicts the study area within the state of Wyoming.

386 (OpenStreetMap basemap: http://www.openstreetmap.org/copyright [32].)

387

388 **Seasonal boundaries**

389 As no Clark's Nutcrackers bred in 2011, I based seasonal boundaries on breeding years

390 2010 and 2012. Based on my observations of Clark's Nutcracker behavior, the prebreeding

391 season ranged from January 15, the first date I trapped Clark's nutcrackers, through March 4.

392 The breeding season is considered March 5, the first date in any year a Clark's nutcracker was

393 seen building a nest, through June 15, the last date a nestling was observed on a nest.

394 **Determination of breeding versus nonbreeding years**

395 To evaluate breeding status and breeding activity of individuals and within the population, I

396 used trapping, radio tracking, surveying, and documentation of fledglings and older young of the

397 year. First, I examined each trapped bird to determine if a brood patch was present. Second, at all

398 times while in the field, I documented all breeding activity of radio tagged and unbanded Clark's

399 nutcrackers, including courtship behavior (Table 2.1), nest building, and nest attendance. Third, I

400 documented all observed fledglings and older young of the year at all times while in the field.

401 **Table 2.1. Courtship Behavior.**

402 Courtship behavior includes one or a combination of the following activities and/or calls.

ACTIVITIES	Reference
Bowing	[17,18]
Tail wagging	T. D. Schaming, personal observation
Opening and closing bill while pumping legs	T. D. Schaming, personal

	observation
Neck stretching	[17,18]
Hopping close together on branch with bills open	T. D. Schaming, personal observation
Wild, rapid flights; chasing, flying directly at one another, and making direct contact in air while both flap their wings	[18,29], T. D. Schaming, personal observation
One crouching, stretching out and fluttering wings, other feeding	[17,18]
Carrying sticks while performing other courtship displays	[17,18]
CALLS	
Courtship begging	[17,18]
Musical or chirrup	[17,18]
Hiccup	[17]
Crackle- and- whistle or crackle	[17,18]
Pop-click	[17]
Bullfrog or croaking	[17,18]

403

404 The easiest way to document breeding in the population is to document observed
405 fledglings. Fledglings are easy to differentiate from adults: they have a noticeably shorter beak
406 and shorter tail; no white on their face, around their bill and eyes; a duller body, wings and tail,
407 with more brown – grey plumage; and when recently fledged, pink spots below their eyes, a red
408 mouth, and grey legs and irides [17]. The young birds are also conspicuous because of their loud,
409 regular begging calls [18,33], and their distinctive flying, landing, foraging and social behaviors
410 (T. D. Schaming personal observation). During the breeding and post-breeding seasons,

fledglings (fledged at the site) and/or older young of the year (either fledged at the site or dispersed in from outside the study area, appearing in August or later) were observable. Fledglings are readily recognizable in May through July, and older young of the year are discernible into the autumn. Years in which I observed brood patches, nesting activity and/or presence of fledglings were considered breeding years.

Capture and marking

Trapping sites were located within the same three general locations in all years. The first was in high-elevation whitebark pine habitat with some subalpine fir (2,659-2,757 m). The second was in mid-elevation lodgepole pine habitat with some Douglas-fir and Engelmann spruce (2,187-2,265 m), and the third was in mid-elevation Douglas-fir habitat with some subalpine fir and limber pine, and Englemann spruce - lodgepole pine habitat (2,131-2,259 m; Fig. 2.1). In 2011, I attempted to trap at a fourth location in low- to mid-elevation Douglas-fir habitat with limber pine and lodgepole pine (1,763 – 2,208 m), at which I never observed a Clark's nutcracker at or near the trapping sites. In 2011, I also trapped at a fifth location in a residential area (2097 m), at which I banded, but did not radio tag any birds. I chose the trapping site locations because they represent all possible conifer habitats, and were accessible, within forty-five minutes from the nearest parking area.

At each of the trapping sites, I baited the Clark's nutcrackers with beef suet and trapped adults in mist nets or bow nets. I weighed (g, 1 decimal place) and measured (culmen (tip of the upper mandible to the first feathers; mm, 1 decimal place), tarsus (bent right leg; mm, 1 decimal place), wing chord (natural curvature; mm, 0 decimal places), and tail (base of tail to tip of longest feather, natural curvature; mm, 0 decimal places)) adults to determine body condition index. I banded each with a U.S. Fish and Wildlife Service aluminum band and three colored leg

bands. I determined the amount of body fat with a furcular fat score of 0 – 5 (0 = no fat, 1 = 1 – 5%, 2 = 6 – 33%, 3 = 34- 66%, 4 = 67 – 100%, 5 = bulging), and documented if a brood patch or *cloacal protuberance* were present. Both males and females have brood patches [34]. A lack of a brood patch indicated that the individual was not breeding at the time of capture; it was not a reliable indicator of whether an individual bred at some time during the season. I weighed, measured, and banded young on the nest.

I attached 3.9 g (three percent of body weight) VHF radio transmitters (Advanced Telemetry Systems (ATS), Isanti, Minnesota, USA) to a subset of Clark's nutcrackers with backpack harnesses. Due to logistical constraints, I did not randomly select birds to radio tag from among those captured.

Radio tracking

In 2010, I primarily triangulated the radio tagged Clark's nutcrackers' locations, and opportunistically attempted to home in on individuals. In 2011 and 2012, with the aid of field assistants, I primarily obtained point locations on Clark's nutcrackers by homing. I attempted, when possible, to closely observe each radio tagged bird for a minimum of two hours each week, until the end of the field season (Table 2.2) or until an individual's signal "disappeared". If a signal was not heard, I continued to listen for it daily until I observed that the bird was alive, but had a broken antenna, or until the end of the field season. Antennas may have snapped due to preening; I observed individuals preening the antenna along with the feathers several times, and observed antennas which were curled rather than straight, likely due to preening. On eleven occasions, I searched for "missing" birds using dual wing-mounted H antennas attached to an airplane. During all observations while homing, I documented the activity budget (e.g. foraging, flying, perching, breeding activity), and habitat. I recorded all activities on initial observation of

the individual, then continuously throughout the observation period, noting all times when the activity changed.

Table 2.2. Annual variation in documentation of population-wide breeding.

Between years, there was variation in the dates and number of days I spent in the field, the number and dates of Clark's nutcrackers trapped, the number radio tagged, and the number of days radio tagged birds were observed. Nonbreeding years are in bold.

Year	Dates in field	# Trapped (Dates trapped)	# Radio tagged	Mean # days radio tagged birds observed	# Person-days (breeding and post-breeding seasons)
2009	**Mar 6 - Nov 2**	**38 (Mar 24 – Apr 20)**	**0**	**NA**	**102**
2010	Mar 7 - Aug 19	15 (Mar 17 – May 27)	13	4 ± 1	99
2011	**Jan 11 – Nov 20**	**67 (Jan 28 – Jun 27)**	**29**	**19 ± 2**	**327**
2012	Jan 7 – Oct 31	35 (Jan 15 – Mar 11)	34	17 ± 1	282
2013	May 19 – Oct 1	0 (NA)	0	NA	157

I located nests by tracking radio tagged Clark's nutcrackers to the nest and through incidental observations. By tracking radio tagged birds, I was able to observe each bird in all used habitats, and therefore habitat specific detectability did not play a role in locating radio

tagged birds' nests. I regularly monitored each active nest, each nest at which Clark's nutcrackers were observed building, or where eggs or nestlings were present. I recorded the number of eggs and young, and estimated the age of young at each visit. When logistically feasible, I visited each nest after laying was complete to count the final clutch size, close to the estimated hatching date to determine the number of young hatched, between 13 and 17 days after hatching to band young, then between 22 and 28 days, the time period when fledging occurs (T. D. Schaming personal observation). In between, I opportunistically monitored nests when I followed radio tagged individuals to the site, or when I was close to the location. I considered young successfully fledged if I observed fledglings off the nest, likely fledged if the nest was empty within 22-28 days post-hatching, or fledging status unknown if nests were not checked within 22-28 days post-hatching, but were empty after 28 days. At all times while radio tracking, I recorded all observed fledglings and older young of the year.

I cannot reasonably compare proportion of breeding birds, number of breeding attempts, number of nests located, or number of fledged young between 2010 and 2012 because the sampling regimens were different. It is likely that I did not observe the majority of breeding attempts by radio tagged birds in 2010 because I did not home to individuals on a regular basis. However, in 2011 and 2012, it is unlikely that I missed breeding attempts because I routinely homed to individuals.

I tracked Clark's nutcrackers using R410 digital scanning receivers (ATS), and a three element folding Yagi (ATS; AF Antronics, White Heath, Illinois, USA) or H (ATS) handheld antenna, and recorded the locations of individuals using portable global positioning system (GPS) units (Garmin International Inc., Olathe, Kansas, USA; Universal Transverse Mercator Zone 12N, NAD 1983).

Occupancy surveys

My protocol for establishing occupancy survey points evolved between years, based on experience and logistical constraints. In 2009, I located 48 points along eight 1 km transects. Transects were not set up on trails or roads. I grouped the points on transects so that I could walk between points in one day. The starting locations were randomly chosen from two focal areas within whitebark pine habitat, within sixty minutes of driving, and ninety minutes of hiking. Transect direction was randomly determined by spinning a compass rosette, avoiding paved roads, rivers and cliffs. To maintain spatial independence, each transect was spaced a minimum of 500 m apart, and each point on a transect was spaced 200 m apart, a standard distance for passerine point count surveys [35]. Though each starting location was in whitebark pine habitat, the ecosystem where I work is a mosaic of habitats. Habitats on the transects and traversed en route to the transects included all conifer habitats at the study site.

In 2011, I established 39 additional points within four focal areas. I located three focal areas at sites within a sixty minute drive of Jackson, WY; two had whitebark pine habitat within ninety minutes of a road, and one had only sparse whitebark pine habitat within 30 km. All six conifer habitats were represented in at least one focal area. I established 12, 12, and 10 random points within each area in conifer habitat, at least 400 m apart, using a random point generator (http://www.geomidpoint.com/random/). I also located two arbitrary points in the area with sparse whitebark pine habitat. I established three random points in a fourth focal area with whitebark pine, a 120 minute drive from Jackson, WY.

In 2012, I established nine additional points in three focal areas (four, three and two points) with whitebark pine as the dominant species. I randomly picked a starting point in each focal area, randomly picked the direction of the transect by spinning a compass rosette, then set

up points 400 m apart. If blocked by a river, cliff, or other obstacle, I spun the compass again, and followed the first random direction greater than 45 degrees from direction of the last point. I also established seven arbitrary points in whitebark pine habitat near citizen science point count survey locations.

In 2013, to ensure the survey results were representative of the ecosystem, I established 134 additional points in locations throughout Bridger-Teton and Shoshone National Forests. I divided the two national forests into 30 equal sized focal areas. In 25 of the 30 focal areas (areas which did not already have six previously established points, were open to the public, and within ninety minutes from a road), I picked a random starting point in or within 2 km of whitebark pine habitat, then set up an additional two to five points, each 400 m apart, in a randomly chosen compass direction. I set up six, five, four or three points in seventeen, three, two and three areas. I also added ten additional points on two transects in a focal area established in 2012.

Each year, 2009 through 2013, I conducted point count surveys at newly established points and a subset of points established in previous years. During the surveys and while hiking to the survey locations, I recorded all observed fledglings and older young of the year.

Fledgling surveys

In 2012, I conducted fledgling surveys in two locations, one with a mosaic of all six conifer habitat types, and the second in Douglas-fir forest. I hiked in an arbitrary direction from the parking area, avoiding locations previously traversed, documenting the time and location of each fledgling seen or heard, the number of juveniles in a group, and the habitat at each siting.

Habitat classification

To determine habitat at survey points, I used a modified point quarter method at each survey location. From the primary survey point, then from four points 30 or 35 m to the

northwest, northeast, southwest and southeast, I divided the area into four quadrants, along north-south and east-west axes. The distance of 30 or 35 m varied between years due to an error on the data sheets. In each quadrant at each of the five points, I documented the species of, and measured the circumference of and distance to the closest live tree, and the circumference of and distance to the closest live and dead whitebark pine tree. If no trees and/or no live and/or dead whitebark pine trees were present within 200 m, the quadrant was labeled as empty for that category.

To determine the habitat surrounding active nest or nest building trees, I estimated the proportion of the area within 100 m radius composed of each tree species. I did not conduct a point quarter method at six of the 247 occupancy survey points due to time constraints. I determined the habitat at these six points and at all other locations where I worked with a land cover type map in ArcGIS. I constructed a geospatial layer of land cover types using map data from the whitebark pine stand-level condition assessment [36], the Bridger-Teton National Forest (existveg_2007, USDA National Forest Service Remote Sensing Applications Center, obtained from Grand Teton National Park), Shoshone National Forest (FSVeg Spatial database, extracted March 22, 2012, obtained from U.S. Forest Service Rocky Mountain Region (R2) Regional Office, Geospatial Services), Grand Teton National Park (2005 vegetation mapping report, obtained from Grand Teton National Park), and Wyoming GAP analysis (U.S. Geological Survey Gap Analysis Program- Land Cover Data v2.2 [37]) vegetation maps. When discrepancies occurred, the layers were prioritized in the order listed. For the habitat at the six occupancy survey points at which I did not use a point quarter method, I also included qualitative habitat data on tree species present within 100 m of the point.

Environmental variables

Whitebark pine cone crop was represented by the average number of cones per tree documented by the Interagency Grizzly Bear Study Team's annual cone counts throughout the region (Haroldson personal communication, [38]). Snowpack and temperature were represented by the average daily snow water equivalent (SWE), a measurement of the amount of water contained in the snowpack, and average daily temperature, respectively, during March, the beginning of the breeding season [39].

Statistical Analyses

Breeding as a function of environmental variables

I used generalized linear mixed models (GLMMs) to test factors that were associated with breeding. I predicted that failure to breed would be linked to whitebark pine cone crop the previous autumn. Due to high early breeding season snowpack in the two nonbreeding years, I could not exclude the possibility that snowpack or an interaction between cone crop and snowpack was the driving factor for nonbreeding years. As snowpack is often related to temperature, I also examined the link between nonbreeding years and early breeding season temperature.

Due to the low power of a sample size of five years, I was unable to use one or separate GLMMs to evaluate the significance of whitebark pine cone crop, snowpack, temperature and the interaction between each as predictors for the probability of a breeding versus nonbreeding year. Therefore, to evaluate if nonbreeding years are related to cone crop versus snowpack or temperature, in three separate GLMMs, I evaluated whether a breeding or nonbreeding season significantly predicted the whitebark pine cone crop the previous autumn, snowpack, and temperature (zero-inflated negative binomial, Gaussian and Gaussian distributions, respectively).

I included year as a random factor in each, and transect as a random factor in the model predicting whitebark pine cone crop.

Body condition index

Julian Date is known to affect mass of birds due to variation in food supply [40], and time of day captured is known to affect the mass of diurnal birds due to fasting overnight [41]. Therefore, to evaluate which variables to include in the adult body condition index, I first used a linear model to determine if mass (g) of adult Clark's nutcrackers varied significantly with Julian date, time of day, or quadratic terms of each measure. I only included each individual the first time it was captured over all years (2009-2012). I then estimated relative body condition index as the residuals of body mass regressed against tarsus length, the body size indicator, and Julian date of capture, to correct for body size and date effects.

There is an ongoing debate in the literature on how to measure body condition of live animals [42,43]. The common technique of ordinary least squares (OLS) regression assumes the predictor variable is measured without error. I justify using OLS regression because the predictor variable, tarsus length, has negligible measurement error. First, only I measured each tarsus, eliminating a large source of potential measurement error between field workers. Second, repeatable measurements of the predictor variable increase its accuracy [44,45]. I measured the tarsus twice on each bird to ensure accuracy. In the rare case where measurements differed, I measured the tarsus a minimum of two additional times to ensure the readings were repeatable. A model II reduced major axis regression is recommended as an alternative to OLS regression; however, only one predictor variable is used in a reduced major axis regression [42]. To justify using OLS regression, I compared the OLS regression results of weight as a function of tarsus length only with a model II reduced major axis regression of the same variables. To evaluate if

body condition index residuals significantly predicted fat score, I used a generalized linear model (GLM) with binomial distributions and a logit link function.

I used two-tailed t-tests to test the hypotheses that body condition index would differ between birds trapped during the prebreeding season in breeding versus nonbreeding years, and during the breeding season in breeding versus nonbreeding years. To evaluate if body condition index during the prebreeding or breeding season significantly predicted a breeding versus nonbreeding year, I used separate GLMs with binomial distributions and logit link functions.

To further examine the relationship between weight and Julian date of capture corrected for tarsus length, I conducted three additional linear models to determine if mass of adult Clark's nutcrackers varied significantly with Julian date and tarsus length. One model included all years, the second only breeding years, and the third only nonbreeding years.

Body condition index as a function of environmental variables

To determine if the environmental factors associated with breeding also impact the body condition index, I used GLMMs to evaluate the significance of whitebark pine cone crop, snowpack, and temperature on the body condition index. I conducted three Kendall's rank correlation tests to evaluate correlation between the three environmental variables. Due to the multicollinearity among the predictor variables, I used three separate GLMMs with Gaussian distributions and included year as a random factor in each.

Other

I used R (version 3.1.0) to perform all analyses. I checked for normality and homogeneity of variance, and met all key assumptions underlying application of GLMs and GLMMs. I applied $p < 0.05$ as the significance level, and report values as mean ± standard error of the mean. I include individuals recaptured between years in summary data in Tables 2.1 and 2.2, but only

include an individual the first time it was captured in analyses.

Data

All of my original data from which this article is based are deposited at Figshare http://dx.doi.org/10.6084/m9.figshare.1157837. Whitebark pine cone crop data was obtained from a third party, the Interagency Grizzly Bear Study Team (http://www.nrmsc.usgs.gov/research/igbst-home.htm), and is available upon request from Mark Haroldson (mark_haroldson@usgs.gov). Snowpack and temperature data are available online from the United States Department of Agriculture Natural Resources Conservation Service Togwotee Pass SNOTEL station (http://www.wcc.nrcs.usda.gov).

Results

Capture

My field assistants and I spent 1,109 person-days in the field, including 967 person-days during the breeding and post-breeding seasons (Table 2.2). Between 2009 and 2012, I trapped and banded 155 adult and 30 nestling Clark's nutcrackers. Nine individuals were recaptured in subsequent years. I only observed brood patches on trapped Clark's nutcrackers during the breeding season. Only including data from the first time each Clark's nutcracker was trapped, individuals weighed an average of 130.1 ± 0.9 g (n = 140; range 106.4 – 155.6). The average tarsus length was 36.6 ± 0.1 mm (n = 146; range 33.3 – 38.9). The average culmen length was 38.3 ± 0.2 mm (n = 146; range 31.0 – 44.4). The average wing cord was 188 ± 1 mm (n = 146; range 173 - 201), and the average tail length was 118 ± 1 mm (n = 146; range 101 - 141). Variation in fat levels was very slight, and I only documented scores of 0 (n = 61) and 1 (n = 82). Body condition index residuals did not significantly predict fat levels (n = 143; $\beta = 0.02 \pm 0.02$, p

650 = 0.4).

651 Radio tracking

652 I fit radio transmitters to, then regularly radio tracked 76 adults. In 2010, I only homed in
653 on radio tagged Clark's nutcrackers an average of 4 ± 1 days. On the other hand, in 2011 and
654 2012, I homed in on radio tagged individuals an average of 19 ± 2 and 17 ± 1 days, respectively.
655 In 2010 and 2012, I found a total of 33 active nests (31 of radio tagged birds, 2 of unbanded
656 birds). I observed six nest building activities for which I did not find a final nest (4 of radio
657 tagged birds, 2 of unbanded birds). Three individuals were radio tagged in two different years,
658 the first in 2010 then 2011 (no nesting observed in either year), the second in 2010 then 2012
659 (nesting observed in both years), and the third in 2011 then 2012 (nesting only observed in
660 2012). The habitat surrounding active nest or nest building trees (n = 32 locations measured) was
661 composed of all six conifer species, whitebark pine, limber pine, Douglas-fir, lodgepole pine,
662 Engelmann spruce, and subalpine fir at 53%, 9%, 25%, 47%, 44%, and 66% of the locations,
663 respectively.

664 Occupancy and fledgling survey habitat

665 Between 2009 and 2013, I conducted 1,066 thirty minute occupancy surveys at 247 point
666 count locations (Fig. 2.1). I carried out surveys in all six conifer habitats. I documented
667 whitebark pine, limber pine, Douglas-fir, lodgepole pine, Engelmann spruce, and subalpine fir at
668 52%, 22%, 33%, 38%, 48% and 64% of the 247 survey points, respectively. In 2012, I conducted
669 73.7 hours of fledgling surveys (64.1 hours in a mosaic of all six conifer habitat types, and 9.6
670 hours in Douglas-fir forest).

671

Habitats visited during daily field work

The study site was a mosaic of habitats, and while trapping, radio tracking, conducting occupancy and fledgling surveys, and hiking to survey locations, I regularly worked in all six conifer habitats at the site (Table 2.3).

Table 2.3. Percentage of days spent in each conifer habitat during the breeding and post-breeding seasons, seasons when it would have been possible to observe evidence of breeding. Numbers do not add up to 100% because I spent time in multiple habitats every day.

Year	Whitebark pine (%)	Limber pine (%)	Douglas-fir (%)	Lodgepole pine (%)	Engelmann spruce (%)	Subalpine fir (%)
2009	70.6	26.5	60.8	49.0	64.7	94.1
2010	48.5	53.5	92.9	77.8	92.9	90.9
2011	52.3	44.0	85.0	85.3	79.2	86.9
2012	67.0	39.7	65.2	67.0	62.4	92.2
2013	72.0	46.5	62.4	71.3	77.7	83.4

Determination of breeding versus nonbreeding years

During the five-year study, I did not observe any indications of individual Clark's nutcrackers attempting to breed at our study site in two years, 2009 and 2011 (Table 2.4). On the other hand, in 2010, 2012 and 2013 I observed multiple indications of Clark's nutcrackers breeding. We, however, did observe courtship behavior in 2010, 2011 and 2012, during both breeding and nonbreeding years, but only during the three years in which I radio tagged and

regularly observed individual birds for long periods of time. Each spring, I contacted local bird watchers, personnel at six local wildlife-oriented nonprofits, the Wyoming Game and Fish Department, and Grand Teton Nation Park to request people contact me with observations of Clark's nutcracker breeding behavior. In nonbreeding years, no-one had observed fledgling Clark's nutcrackers, and no-one came forth with observations at a later date. However, in each of the three breeding years, local citizens emailed with anecdotal observations of Clark's nutcracker fledglings. These observations were consistent with my determination of breeding versus nonbreeding years.

Table 2.4. Annual indications of Clark's nutcracker breeding. Nonbreeding years are in bold.

Year	Fledglings seen on study area	% Trapped adults with brood patches	# Radio tagged observed to attempt breeding	# Active nests observed	# Active nest building observations, final nest not found	Dates nesting activities observed
2009	**No**	**0% (0/38)**	**NA**	**0**	**0**	**NA**
2010	Yes	40% (6/15)	13% (2/13)	2	0	Mar 17-May 4
2011	**No**	**0% (0/67)**	**0% (0/29)**	**0**	**0**	**NA**
2012	Yes	6% (4/65)	88% (30/34)	31	6	Mar 5 – Jun 15
2013	Yes	None trapped	NA	0	0	NA

In 2010, no young fledged from the observed nests (0/2). In 2012, young fledged from a

minimum of 32% (10/31) and a maximum of 39% (12/31) of the active nests. I observed fledglings of radio tagged birds up to approximately 44 days after fledgling (n = 30 nestlings banded). During fledgling surveys, I observed one group (one or more fledglings together at one location) of fledglings every 8.2 hours (n = 73.7 hours; 0.12 ± 0.04 groups per hour).

Breeding as a function of environmental variables

Clark's nutcrackers at the study site experienced large inter-annual differences in food availability and spring snowpack (Figs. 2.2 and 2.3). The average whitebark pine cone crop was lower in the nonbreeding years (8.0 ± 1.7 and 5.2 ± 0.7 cones per tree) than the breeding years (46.5 ± 5.9, 19.8 ± 1.7 and 33 ± 3.7 cones per tree). However, the range of cones per tree (0 – 124) in 2012, a breeding year, fell within the range of cones in 2009, a nonbreeding year (0 – 161). Population-wide failure to breed was a significant predictor of a low cone crop the previous autumn (n = 944; $\beta = 1.5 \pm 0.3$, $p < 0.001$), and a high average daily March snowpack (n = 155; $\beta = -196.3 \pm 62.6$, DF = 3, $p = 0.05$), but did not statistically predict average daily March temperatures (n = 155; $\beta = 1.3 \pm 1.5$, DF = 3, $p = 0.45$).

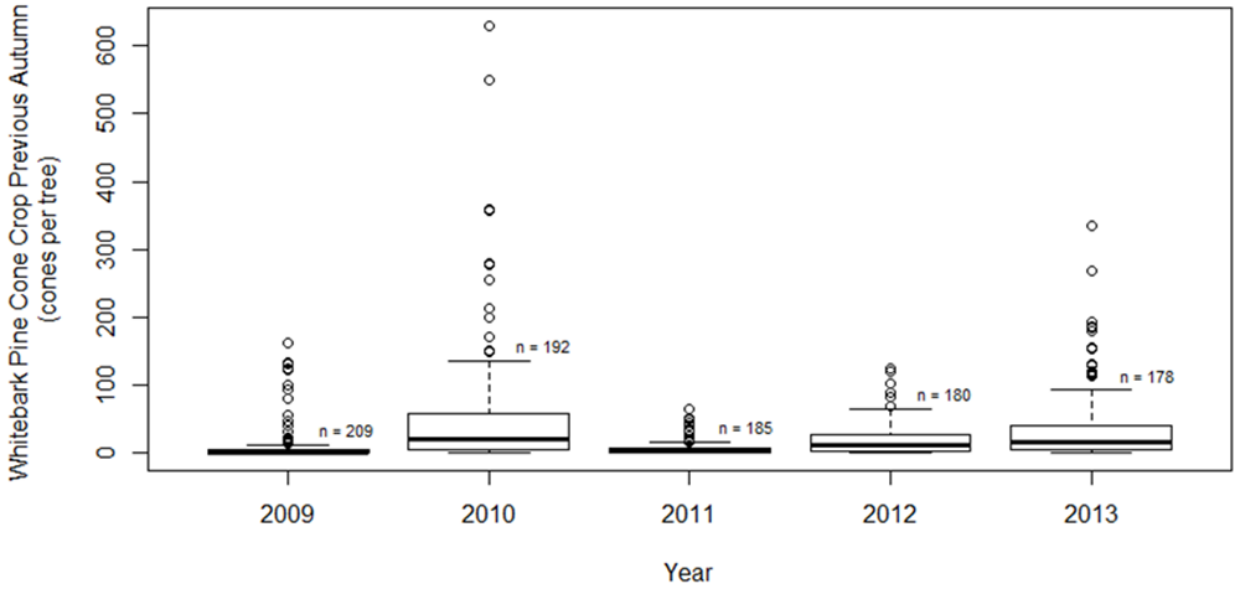

Figure 2.2. Whitebark pine cone crop in breeding versus nonbreeding years. Evidence suggests Clark's nutcrackers did not breed population-wide in 2009 and 2011, years following low whitebark pine cone crops.

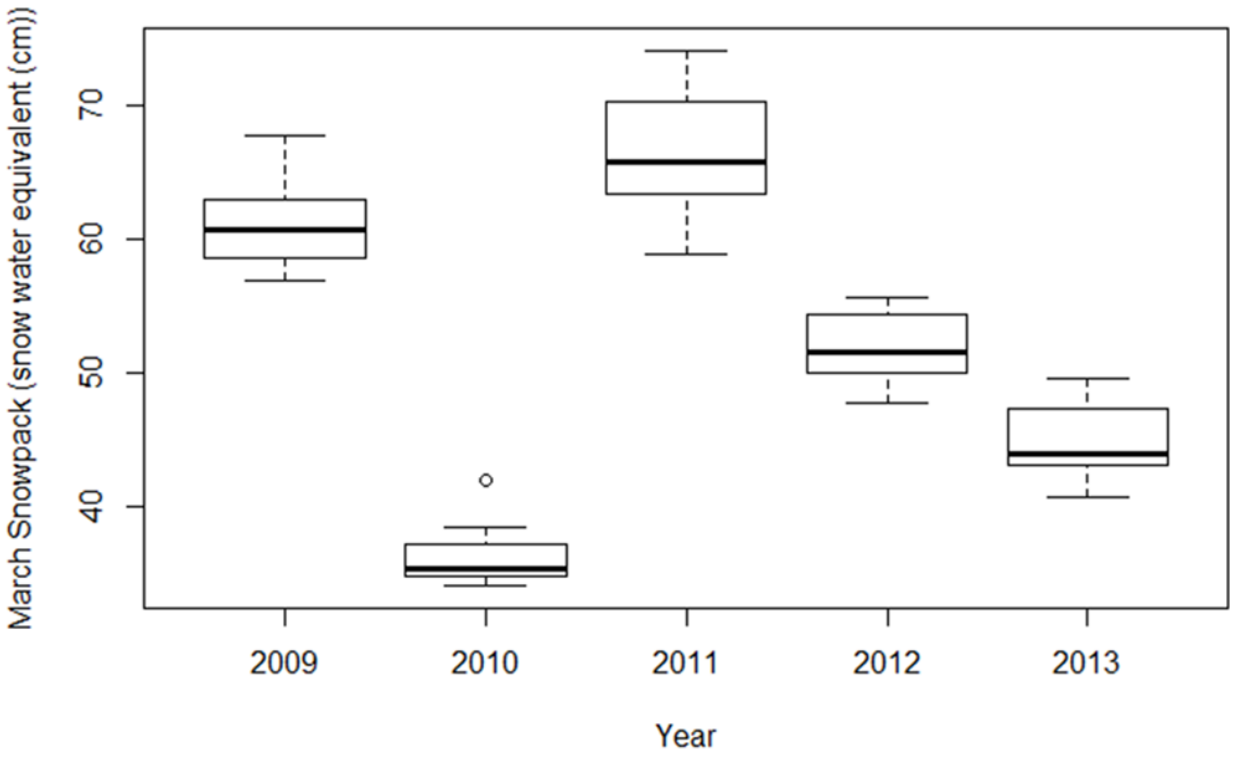

Figure 2.3. Snowpack in breeding versus nonbreeding years. Evidence suggests Clark's nutcrackers did not breed population-wide in 2009 and 2011, years with high average March snowpack (n = 31 for all years).

Body condition index

I trapped Clark's nutcrackers during four prebreeding seasons (2009-2012), two breeding seasons (2011-2012), and one post-breeding season (2011). Both the OLS and model II reduced major axis regressions of weight as a function of tarsus length showed a significant positive

correlation, justifying the use of an OLS regression to determine body condition index ($n = 140$; $\beta = 4.4 \pm 0.9$, $p < 0.001$ and $R^2 = 0.14$, slope = 17.2, angle = 86.7, $p = 0.02$, respectively). Over all years, mass decreased significantly with Julian date of capture ($n = 140$; $\beta = -0.08 \pm 0.03$, $p = 0.001$). However, mass did not vary significantly with time of day captured, or the quadratic terms of each measure (p's > 0.05). Therefore, I estimated body condition index as the residuals of body mass regressed against tarsus length and Julian date of capture, to correct for body size and date effects.

Between breeding and nonbreeding years, adult prebreeding season body condition index did not differ significantly ($n = 43$; $t = 1.8$, $df = 29.7$, $p = 0.09$), and there was similar variability ($n = 26$, $\mu = 2.4 \pm 1.7$, range = -21.3 – 18.0, and $n = 17$, $\mu = -3.1 \pm 2.6$, range = -19.9 – 25.4, respectively; Fig. 2.4). On the other hand, breeding season body condition index was significantly higher in the breeding versus nonbreeding year ($n = 96$; $t = 3.4$, $df = 27.4$, $p = 0.002$). However, there was higher variability in the nonbreeding year ($n = 17$, $\mu = 6.2 \pm 2.0$, range = -8.8 – 21.1, and $n = 79$, $\mu = -1.5 \pm 1.1$, range = -26.7 – 23.3, respectively; Fig. 2.4). During the breeding season, some individuals during the nonbreeding year had a body condition index as high as those from the breeding year. Lower adult body condition index during the prebreeding season did not predict a nonbreeding year ($n = 43$; $\beta = 0.06 \pm 0.04$, $p = 0.08$). In contrast, lower body condition index during the breeding season significantly predicted a nonbreeding year ($n = 96$; $\beta = 0.08 \pm 0.03$, $p = 0.007$).

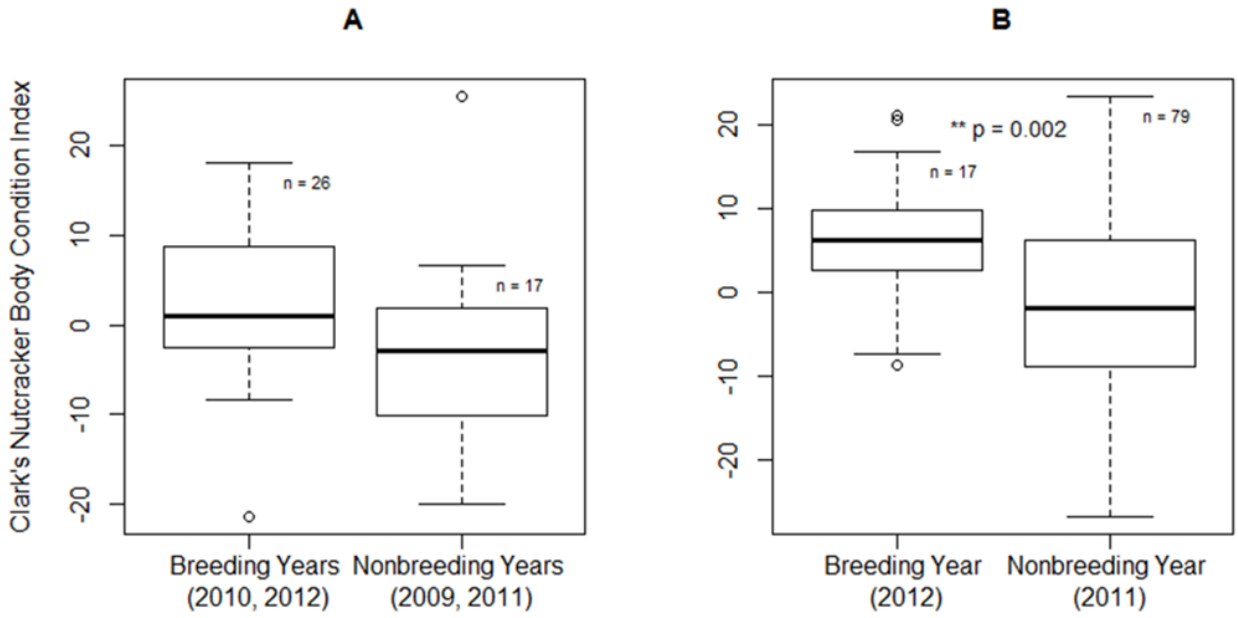

Figure 2.4. Clark's nutcracker body condition index in breeding versus nonbreeding years. The Clark's nutcracker prebreeding body condition index did not differ significantly between breeding and nonbreeding years (A). However, the average body condition index for birds during the breeding season was significantly higher in the breeding versus nonbreeding year (B). Body condition index is the residuals of body mass regressed against tarsus, corrected for date. Clark's nutcrackers were trapped during four prebreeding seasons (2009-2012), but only during two breeding seasons (2011-2012).

Over all years, weight increased significantly with tarsus ($n = 140$; $\beta = 4.12 \pm 0.88$, $p < 0.001$) and decreased significantly with Julian date of capture ($n = 140$; $\beta = -0.08 \pm 0.03$, $p = 0.001$; Fig. 2.5). When examined separately, during breeding and nonbreeding years weight increased significantly with tarsus ($n = 43$; $\beta = 3.8 \pm 1.3$, $p = 0.006$ and $n = 97$; $\beta = 4.1 \pm 1.1$, $p < 0.001$, respectively). During breeding years, though there was a decreasing trend, weight did not decrease significantly with Julian date ($n = 43$; $\beta = -0.05 \pm 0.04$, $p = 0.2$). However, during nonbreeding years, weight did not vary with Julian date ($n = 97$; $\beta = -0.002 \pm 0.04$, $p = 0.96$).

The significance of Julian date over all years, but not during breeding and nonbreedings years separately, is possibly due to the dates of trapping differing during breeding and nonbreeding years (Table 2.2). The average Julian date of capture was 61 ± 5 (n = 43 birds, range = 15 - 136) and 102 ± 3 (n = 97 birds, range = 33 - 178) in breeding and nonbreeding years, respectively.

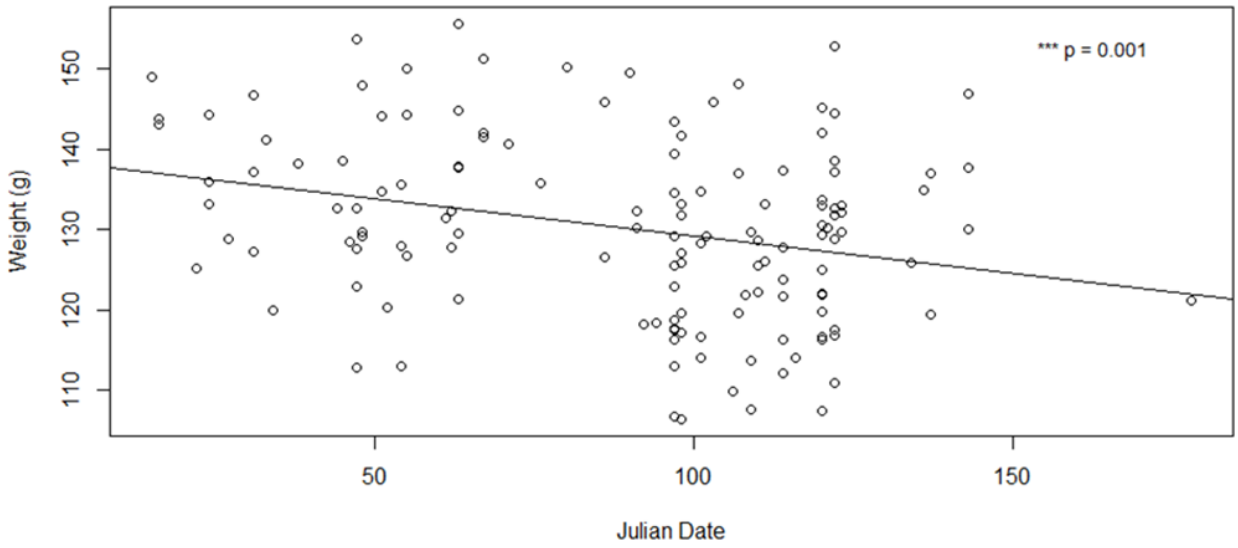

Figure 2.5. Clark's nutcracker weight variation over the trapping season (2009-2012). The weight of trapped Clark's nutcrackers decreased significantly with Julian date of capture.

Body condition index as a function of environmental variables

I determined body condition index for 140 Clark's nutcrackers. The whitebark pine cone crop, average daily March snowpack, and average daily March temperature experienced by the individuals were multicollinear. Cone crop was correlated with March snowpack ($z = -13.7$, $p < 0.001$) and March temperature ($z = 8.9$, $p < 0.001$). March snowpack and temperature were correlated ($z = -8.9$, $p < 0.001$). Clark's nutcracker body condition index was not predicted by whitebark pine cone crop the previous autumn, average daily March snowpack, or average daily March temperatures ($n = 140$; $\beta = 0.2 \pm 0.1$, DF = 2, $p = 0.2$; $\beta = -0.3 \pm 0.2$, DF = 2, $p = 0.2$; and

$\beta = 1.8 \pm 1.6$, DF = 2, $p = 0.4$, respectively).

Discussion

During two of the five years of the study, I had strong evidence suggesting that the Clark's nutcrackers did not breed population-wide in any of the diverse conifer habitats within my study area. I did, however, observe Clark's nutcracker courtship displays in both breeding and nonbreeding years. Clark's nutcracker courtship displays, as in many avian species, occur throughout the year, likely as a means of reinforcing pair bonds [17,46]. Therefore, it is not inconsistent that courtship was observed in nonbreeding years. Elucidation of the specific ecological triggers and exact causal mechanisms underlying absence of breeding will require long-term studies. However, as predicted, nonbreeding years followed autumns with low whitebark pine cone crops. This result is confounded by high average March snowpack in the two nonbreeding years. Consequently, I cannot separate the effects of cone crop and snowpack. Low whitebark pine cone crop, high snowpack, or an interaction between the two, may have influenced the population-wide nonbreeding. They may have provided environmental cues available to the birds prior to breeding which allowed them to predict that breeding conditions would be poor due to low food, leading to the decision to skip breeding. On the other hand, they may have resulted in low body energy stores, leading all individuals to choose not to or be unable to breed. Clark's nutcrackers are long-lived birds, living up to 17 years in the wild [47]. Therefore, adaptively skipping reproduction during resource poor years is consistent with life history theory and maximization of lifetime reproductive success [3,4].

It is possible that Clark's nutcrackers may shift their habitat selection in years with high versus low whitebark pine cone crops, and behavior may vary in different habitats. However, I eliminated bias in assessing breeding behavior within the population by regularly observing

Clark's nutcracker behavior in all six conifer habitats present with my study area each year. Clark's nutcrackers are known to irrupt in years with cone crop failure [20,21], and a portion of the local population may have emigrated from the study area due to low whitebark pine cone crop. However, a number of Clark's nutcrackers did stay in the study area each year. During breeding years, I located nests in areas which contained all conifer types. Because I observed nutcracker behavior in each conifer habitat each breeding and post-breeding season, I should not have missed evidence of Clark's nutcracker breeding in any of the six conifer habitat types during nonbreeding years due to biased sampling.

Whitebark pine is an important Clark's nutcracker food source in the Greater Yellowstone Ecosystem. The two other primary foods, limber pine and Douglas-fir were unlikely to have played a significant role in breeding decisions. Limber pines at the site were few and patchy. Though they are an important late summer food source, the majority of seeds are eaten immediately rather than cached (T. D. Schaming personal observation). On the other hand, the Douglas-fir cone crop was consistently high throughout the study site each year (T. D. Schaming personal observation). However, despite Clark's nutcrackers regularly foraging on Douglas-fir, the seeds contain much less nutrition than whitebark pine seeds (0.06 versus 1.19 kcal per seed, respectively; [48,49]). Clark's nutcrackers are estimated to require 11,827 kcal to survive from mid-October through mid-April, when alternative foods become available [26]. Therefore, an individual requires 9,939 whitebark pine seeds or 197,117 Douglas seeds to survive each winter. Clark's nutcrackers cache substantially more seeds because some may spoil or will escape through germination, rodents may steal caches, some caches may become inaccessible or may not be relocated, and some may be needed to feed young [26]. Consequently, though Douglas-fir are more numerous, the increased handling time per seed (24.3 versus 4.9 s/seed for whitebark

pine [16,49]) and quantity of seeds they would require to survive the winter, it is unlikely that they could replace whitebark pine in the diet.

Barringer et al. [50] determined that Clark's nutcrackers visit whitebark pine stands with lower cone production less frequently, resulting in a lower probability of seed dispersal in such stands. A low whitebark pine cone crop would lead to both fewer seeds available to be cached and lower visitation by Clark's nutcrackers. The Clark's nutcrackers would therefore have less food, fewer cached whitebark pine seeds, to feed themselves and their young over the winter and following spring. Clark's nutcrackers slowly lose their memory of their seed caches after 183 days, and many seeds remaining after the first year would have germinated, spoiled or been robbed by other animals. Thus, they would not be able to rely on cached seeds from years other than the most recent autumn [19]. Due to fewer seed caches, the birds may also have been forced to travel farther to find alternative food if adequate supplies of cached seeds were not available on their breeding territories. This may not have been possible if they needed to return regularly to a nest.

Snowpack may also play a role in Clark's nutcrackers skipping breeding. Snowpack may have made it difficult to retrieve seeds cached underground or to forage for other types of supplementary food. However, Clark's nutcrackers do retrieve caches from under the snow (T. D. Schaming personal observation, [51]). They cache up to 59% of seeds aboveground [52], and regularly cache in exposed areas, such as steep cliffs and south facing slopes, where wind and sun prevent heavy snow accumulation [26,29,49]. Even during the springs with high snowpack, I regularly observed Clark's nutcrackers using locations with both bare, exposed slopes and deep snowpack.

To my knowledge, there is no evidence that high snowpack prevents Clark's nutcrackers

from nesting in a given year. High snowpack seems more likely to influence when the birds can start breeding, rather than their overall tendency to skip breeding [51]. Nest building dates from populations in diverse geographical locations vary from mid- to late January in British Columbia through June 1 in the eastern Sierra Nevada, CA [51,53]. In fact, Clark's nutcrackers are primarily found in high, mountainous areas [17], and nests have been found in locations with deep snow (e.g. [18,54]). I regularly observed Clark's nutcrackers during the breeding season in habitats with high snowpack. Between years, I often observed individuals in the same, snow-covered locations regardless of the interannual variation in snowpack.

Previous authors have suggested the Clark's nutcrackers may forego breeding in years with low food, but this is the first study to positively document it [18,26]. Foregoing breeding may be an adaptive strategy of Clark's nutcrackers to face the trade-off between survival and reproduction owing to environmental constraints. Skipping breeding in poor years, years with low resources, such as food or breeding sites, may lead to a higher likelihood of future breeding or survival to a later year. If so, breeding plasticity could be one means for Clark's nutcrackers to maximize lifetime reproductive success while exploiting a variable environment. Such an adaptive strategy, skipping breeding in resource-poor years, is not uncommon among vertebrate species. Pinyon Jay (*Gymnorhinus cyanocephalus*) breeding is only predictable following major cone crops, and some or all do not attempt to nest in the spring after a local cone crop failure, whereas Crossbills (genus *Loxia*) are believed to breed only when there is a high seed supply [9,55]. Dormice (*Glis glis*) stay sexually inactive when beech trees are not masting [56]. Snow petrels (*Pagodroma nivea*) will not breed when severe snow and ice impede access to nesting locations [57], and red-footed boobies (*Sula sula*) are more likely to skip breeding in El Niño years when high sea surface temperatures reduce food supplies [7].

Skipping breeding may be an effective adaptive strategy to face the survival-reproduction trade-off. However, if poor environmental conditions which lead to skipping breeding become more prevalent, individuals may skip breeding more often than in the past. Such an increase could lead to a population decline. Because some habitats may historically have had enough good resource years to maintain populations, individuals may continue to prefer the habitats after the number of poor-resource years increases. This would lead to an ecological trap [58]. If the population-wide failure to breed is caused by low whitebark pine cone crops and Clark's nutcrackers stay in or near the whitebark pine habitats without breeding, the declining whitebark pine habitats may become sink habitats for the birds [59].

Whitebark pine forest communities are rapidly disappearing range-wide, and even some of the healthiest whitebark pine stands, located in the Greater Yellowstone Ecosystem, have severely declined since 1999 (Fig. 2.6) [24]. The decline is primarily due to a mountain pine beetle epidemic that has been worsened by favorable effects of global warming on bark beetle reproduction [60]. In 2009, 46% of these whitebark pine stands were classified as "high mortality" [61]. Clark's nutcrackers regularly experience significant inter-annual differences in food availability because the whitebark pine is a masting conifer; however, because the whitebark pine is declining, the number of whitebark pine seeds available during both masting and nonmasting years is lower. Years with low whitebark pine cone crops occur frequently in the Greater Yellowstone Ecosystem: 44% (15/34) of the years since 1980 had cone crops at or lower than the average levels of the 2009 and 2011 nonbreeding years. Since 1980, 24% (8/34) of the years had a high March 1st snowpack, a level at or higher than the average levels observed in the 2009 and 2011 nonbreeding years. Fifteen percent (5/34) of the years since 1980 had both low cone crops and high snowpack.

Figure 2.6. Dying whitebark pine trees. Example of whitebark pine trees at the study site which are dying due to mountain pine beetle attacks the previous year. (Photo credit: T. D. Schaming)

Whitebark pine cone crop, high snowpack or an interaction with cone crop and snowpack may be the driving force behind the decision to forego breeding. If so, the continuing decline of whitebark pine trees, and the predicted increase in number of years with extreme snow, could have a strong negative effect on stability of the regional Clark's nutcracker population [62]. The proportion of potential breeders that actually breeds affects population growth rate. Therefore, factors which influence the number of breeders can act as a strong regulatory mechanism. Nonbreeding years would have important effects on population size and structure. It is possible

904 that the extreme years in which all individuals in a population fail to breed have more important
905 effects on population size and age structure than "average" years [63,64]. As stated by Anderson
906 et al. [65], "Understanding how patterns of behavior change as landscapes are altered through
907 time may provide important insights into mechanisms underlying observed demographic trends
908 in populations".

909 An increase in the number of Clark's nutcracker nonbreeding years could also have
910 serious ecosystem-wide consequences. Clark's nutcrackers shape the ecosystems in which they
911 live: annually, individuals store tens of thousands of seeds in thousands of separate locations
912 [29,49]. Seeds not retrieved for food are able to germinate [33]. Clark's nutcrackers disperse
913 seeds up to 32.6 km, rapidly and effectively moving seeds longer distances than wind, rodents
914 and all other North American seed hoarding birds. They enable rapid migration of seeds, and
915 contribute to gene flow across and between habitat islands [52]. They often move seeds across
916 latitude and elevation, as well as into disturbed areas [52,66]. Clark's nutcrackers may cache the
917 majority of seeds in areas unsuitable for germination [52]. However, because individuals cache
918 such a high volume of seeds each year, they "plant" many seeds in in microhabitats and local
919 landscapes suitable for germination and establishment [52]. In the face of current climate and
920 habitat change, the long-distance dispersal of conifer seeds, and thus the continued association
921 between Clark's nutcrackers and conifers, may be critical in mitigating against local genetic
922 bottlenecks and inbreeding depression. Such dispersal bolsters effective population size and
923 facilitates rapid colonization of newly available ideal habitats.

924 In ecosystems with increased variability resulting from climate and habitat change,
925 individuals could have a higher probability of encountering poor resource conditions; such
926 conditions would result in a lower probability of successful reproduction and survival [4].

Habitat specialists in particular may be especially vulnerable to such environmental changes if they are unable to adapt. Accurately predicting the impact of both declining habitat and a more variable climate is a major challenge in ecology [4]. It is important to understanding the ecological triggers and exact causal mechanisms of population-wide decisions not to breed; in the face of climate change and environmental disturbance, this information will increase our ability to effectively manage populations and communities.

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CHAPTER 3

CLARK'S NUTCRACKER BREEDING SEASON SPACE USE AND FORAGING BEHAVIOR[2]

Abstract

Considering the entire life history of a species is fundamental to developing effective conservation strategies. Decreasing populations of five-needle white pines may be leading to the decline of Clark's nutcrackers (*Nucifraga columbiana*). These birds are important seed dispersers for at least ten conifer species in the western U.S., including whitebark pine (*Pinus albicaulis*), an obligate mutualist of Clark's nutcrackers. For effective conservation of both Clark's nutcrackers and whitebark pine, it is essential to ensure stability of Clark's nutcracker populations. My objectives were to examine Clark's nutcracker breeding season home range size, territoriality, habitat selection, and foraging behavior in the southern Greater Yellowstone Ecosystem, a region where whitebark pine is declining. I radio-tracked Clark's nutcrackers in 2011, a population-wide nonbreeding year following a low whitebark pine cone crop, and 2012, a breeding year following a high cone crop. Results suggest Douglas-fir (*Pseudotsuga menziesii*) communities are important habitat for Clark's nutcrackers because they selected it for home ranges. In contrast, they did not select whitebark pine habitat. However, Clark's nutcrackers did adjust their use of whitebark pine habitat between years, suggesting that, in some springs, whitebark pine habitat may be used more than previously expected. Newly extracted Douglas-fir seeds were an important food source both years. On the other hand, cached seeds made up a

[2] Schaming, T. D. 2016. Clark's Nutcracker Breeding Season Space Use and Foraging Behavior. PLOS ONE. 11(2): e0149116. doi:10.1371/journal.pone.0149116.

relatively lower proportion of the diet in 2011, suggesting cached seeds are not a reliable spring food source. Land managers focus on restoring whitebark pine habitat with the assumption that Clark's nutcrackers will be available to continue seed dispersal. In the Greater Yellowstone Ecosystem, Clark's nutcracker populations may be more likely to be retained year-round when whitebark pine restoration efforts are located adjacent to Douglas-fir habitat. By extrapolation, whitebark pine restoration efforts in other regions may consider prioritizing restoration of whitebark pine stands near alternative seed sources.

Introduction

For effective conservation, it is important to consider the entire life history of a species [1]. Understanding home range size, territoriality, habitat selection, and foraging behavior is fundamental to predicting a species vulnerability to decline [1,2]. It is also important to the development of management and conservation strategies [1]. In particular, the habitat selected during all important life stages should be considered when designing management plans. For example, neotropical migrants require both specific northern breeding and southern wintering habitats, and spotted salamanders (*Ambystoma maculatum*) breed in vernal pools, then use surrounding woodlands the remainder of the year [3,4]. Sound management strategies may depend on protection of multiple habitat types.

Decreasing populations of five-needle white pines may be leading to the decline of Clark's nutcrackers (*Nucifraga columbiana*) in large parts of their range [5–8]. Previous research has revealed that in whitebark pine (*Pinus albicaulis*) habitat, the frequency of Clark's nutcracker occurrence decreased with lower whitebark pine cone production [7,8]. Fewer five-needle white pines leads to fewer cones, which leads to fewer Clark's nutcrackers. In areas where its primary seed sources are declining, Clark's nutcrackers may increasingly need

alternate seed sources and habitats to support populations.

Large-seeded pines are important foraging habitat for Clark's nutcrackers, because each individual stores tens of thousands of conifer seeds every autumn [9,10]. The birds use the cached seeds for food for both overwinter survival and feeding nestlings, but are estimated to cache two to five times their energetic requirements [9–12]. The importance of specific large-seeded pines to Clark's nutcrackers' diet varies geographically, and all the pines are subject to years of low cone production [6,13,14]. When preferred pines produce few cones, alternative seed sources are essential. Clark's nutcrackers may forage on less preferred local conifer species, or, in years with widespread cone crop failure, birds will move out of the ecosystem [15,16].

In many areas, Clark's nutcrackers use whitebark pine seeds as an important food source [9,17]. Whitebark pine is a keystone species and an obligate mutualist of Clark's nutcrackers [13,14]. It depends on Clark's nutcrackers for dispersal of its wingless seeds [13,14]. This Clark's nutcracker-whitebark pine mutualism is critical to ecosystem function [13,14]. Whitebark pines play an important role in providing important ecosystem services, including providing food and habitat for wildlife, preventing erosion and protecting watersheds [5,18–20]. Currently, whitebark pine forest communities are rapidly disappearing range-wide due to decades of fire suppression, widespread infection by the non-native fungal pathogen *Cronartium ribicola*, which causes white pine blister rust, and outbreaks of mountain pine beetles (*Dendroctonus ponderosae*) [13]. Consequently, extensive efforts are in place to restore whitebark pine, with the assumption that Clark's nutcrackers will continue to be available to disperse the whitebark pine seeds [21]. It is vital to protect Clark's nutcracker populations because they are important seed dispersers for not just whitebark pine, but for at least ten conifer species in the western U.S. [22]. The continued dispersal of pine seeds by Clark's nutcrackers

1168 increases the regeneration capacity of the declining five-needle pines.

1169 Previous research in whitebark pine ecosystems has documented the importance of
1170 multiple conifers, including ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), and
1171 Douglas-fir (*Pseudotsuga menziesii*), to Clark's nutcrackers during the autumn harvest season
1172 [17,22,23]. When whitebark pine cone crops are depleted, the birds begin harvesting other
1173 locally available seeds [17]. Clark's nutcracker breeding season activities are also intimately
1174 linked to the autumn harvest. During the breeding season, seeds cached the previous autumn are
1175 consumed by adults and nestlings [11,24,25]. Also, in the Greater Yellowstone Ecosystem,
1176 where whitebark pine is the predominate large-seeded conifer, previous research suggests that
1177 Clark's nutcracker populations do not breed in years following low whitebark pine cone crops
1178 [26]. Understanding Clark's nutcracker breeding season space use and foraging behavior in
1179 whitebark pine ecosystems – particularly the variation between years following low vs. high
1180 whitebark pine cone crops – is essential to our understanding of how Clark's nutcrackers can
1181 persist in these declining ecosystems. Despite its importance, Clark's nutcracker breeding season
1182 space use is poorly studied [6,27].

1183 Clark's nutcracker breeding habitat varies geographically [6]. Clark's nutcrackers breed
1184 in multiple forest communities including piñon-juniper woodland (*Pinus edulis* and *Pinus*
1185 *monophylla,* and *Juniperus* spp.), ponderosa pine, Douglas-fir, Jeffrey pine, and mixed
1186 coniferous subalpine communities which include whitebark or limber pine (*Pinus flexilis*) [See
1187 6]. Observational studies suggest that during the breeding season, whitebark pine communities
1188 are used infrequently. Nonetheless, all of the breeding habitats used include conifer seed sources.
1189 In the only previous systematic study of space use of radio-tracked Clark's nutcrackers, breeding
1190 season space use and foraging behavior were not separately evaluated [22,27].

My objectives were to evaluate Clark's nutcracker breeding season home range size, territoriality, habitat selection, and foraging behavior in the southern Greater Yellowstone Ecosystem, a region with large-scale whitebark pine decline [28]. I assessed territoriality because evidence of territoriality would influence both home range size and habitat selection. I examined individual behavior over two years, a nonbreeding and a breeding year [26]. The nonbreeding year followed an autumn with a lower whitebark pine cone crop and had a higher spring snowpack compared to the breeding year [26]. By focusing on two years with diverse demographic and environmental conditions, I evaluated a wider range of behavioral responses. By working in a region with extensive mortality of whitebark pine, the results will aid in understanding the range of responses that Clark's nutcracker populations exhibit as the habitats and the resources they provide are lost. This information will contribute to the creation of more effective management strategies.

Materials and Methods

Ethics statement

I captured and handled all birds according to Animal Care Protocol guidelines approved by Cornell University. This research was approved by the Cornell University Institutional Animal Care and Use Committee (protocol # 2008-0176). I banded Clark's nutcrackers under U.S. Fish and Wildlife Permit # 23533, and Wyoming Game and Fish Chapter 33 Permit # 695. I conducted all field work under U.S. Forest Service Special-Use Authorization # JAC747002 (2009-2013) and Grand Teton National Park Scientific Research and Collecting Permit #'s GRTE-2011-SCI-0052 and GRTE-2012-SCI-0069.

Field Methodology

Study area

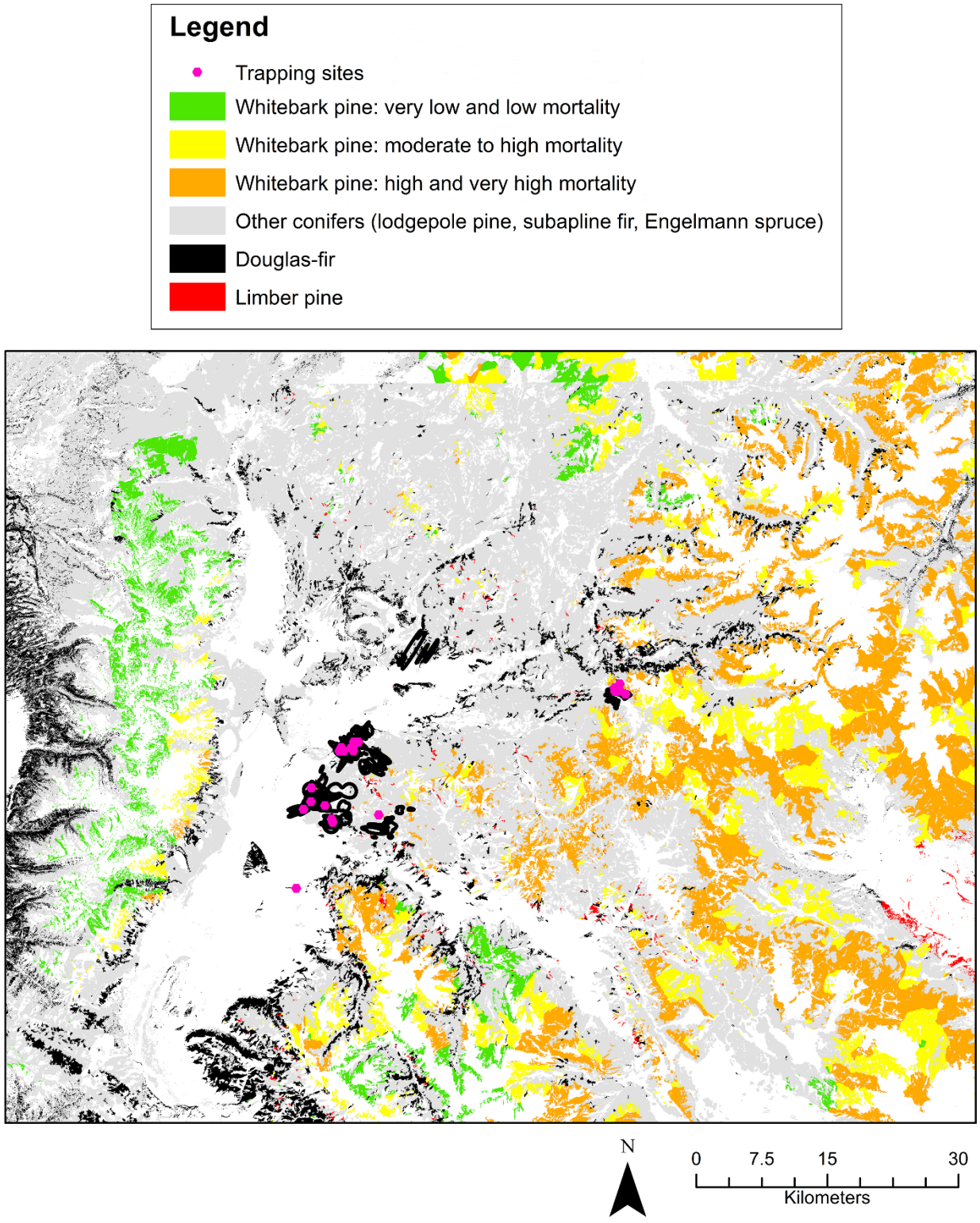
Between 2009 and 2015, I studied Clark's nutcrackers in the southern Greater Yellowstone Ecosystem, primarily in Bridger Teton and Shoshone National Forests, and Grand Teton National Park (25,050 km^2). This portion of the study is based on the years 2011-2012, the only years in which I intensively radio-tracked and conducted regular behavioral observations of radio-tagged Clark's nutcrackers. It was predominantly conducted in the area bounded by 43º56'10" N north, 43º34'34" N south, 110º38'20" W west, and 110º04'59" W east (~1,220 km^2). The forested habitat primarily consists of six conifer species: whitebark pine, limber pine, Douglas-fir, lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea englemannii*), and subalpine fir (*Abies lasiocarpa*). The conifer habitat is intermixed with aspen (*Populus tremuloides),* sagebrush (*Artemesia tridentata*), grassy open areas, high mountain meadows and rocky outcroppings.

Seasonal boundaries used in this study

I based seasonal boundaries on breeding years 2010 and 2012 because I did not observe breeding Clark's nutcrackers in my study area in 2011. The prebreeding season ranged from January 15, the first date I trapped Clark's nutcrackers, through March 4. The breeding season is considered March 5, the earliest date I observed a Clark's nutcracker building a nest during the study, through June 15, the last date I observed a nestling on a nest (S3.1 Fig). The seed preharvest season is the time period during which Clark's nutcrackers were eating immature whitebark pine seeds, but not yet caching mature seeds. It began June 16 and ended the day prior to my first observation of a Clark's nutcracker with a full sublingual pouch each year, August 8, 2011 and July 29, 2012.

Capture and marking

Each year, I located trapping sites for radio-tagging Clark's nutcrackers within the same three general areas (Fig. 3.1). The first set of sites was in high-elevation whitebark pine habitat with some subalpine fir (2659-2757 m). The second set was in mid-elevation lodgepole pine habitat with some Douglas-fir and Engelmann spruce (2187-2265 m). The third set was in mid-elevation Douglas-fir habitat with some subalpine fir, and Engelmann spruce - lodgepole pine habitat (2131-2259 m). These habitats were defined based on a simple assessment at each trapping location. I documented all conifer types visible from the location, then defined dominant trees as those composing greater than 50% of the total visible trees.



1245

1246 **Figure 3.1. Trapping locations, individual home ranges, and available habitat.**

1247 Only trapping sites where individuals were successfully captured are shown. Specific whitebark

1248 pine categories were merged for better visualization. Burned habitat is not shown because it is
1249 not possible to see at the scale of the map.
1250
1251 I trapped adults in mist or bow nets, using beef suet as bait, between January 28 and June
1252 27, 2011 (n = 67) and January 15 and March 11, 2012 (n = 35). I collected body measurements
1253 and color-banded each trapped bird [26]. I attached 3.9 g (less than three percent of body weight)
1254 VHF radio transmitters (Advanced Telemetry Systems (ATS), Isanti, Minnesota, USA) with
1255 backpack harnesses to 29 and 34 of the adults in 2011 and 2012, respectively. Due to logistical
1256 constraints, I did not randomly select birds to radio-tag from among those captured. I excluded
1257 birds trapped adjacent to houses (n = 33), injured birds (n = 1; swollen foot), and birds trapped
1258 when additional radios were unavailable in the field (n = 5).
1259 **Radio-tracking**
1260 I radio-tracked Clark's nutcrackers using homing techniques [29]. I used a digital
1261 scanning receiver (R410, ATS), and a three element folding Yagi (ATS; AF Antronics, White
1262 Heath, Illinois, USA) or H (ATS) handheld antenna. I attempted, when possible, to closely
1263 observe each radio-tagged bird for a minimum of two hours each week until the end of the field
1264 season. If I did not hear an individual's signal, I continued to listen for it daily until I relocated
1265 the bird, visually observed that the bird was alive but had a broken antenna (i.e. the antenna had
1266 snapped and the signal was no longer being transmitted), or until the end of the field season. On
1267 eleven occasions, I attempted to relocate "missing" birds from a fixed wing aircraft using dual
1268 wing-mounted H antennas. During all observations, I documented the spatial coordinates of
1269 every location used by the bird, the microhabitat (e.g., ground, log, tree), and if in a tree, what
1270 tree species and what location in the tree (e.g., bark, foliage). I recorded its activity (e.g.,

foraging, flying, perching, breeding activity), the length of time it was engaged in the activity, and when possible, the food type if foraging (e.g., cached seeds, invertebrates). Unfortunately, due to logistical constraints, it was generally not possible to count the number of food items eaten during each foraging bout. I recorded locations using a portable global positioning system (GPS) unit (Garmin International Inc., Olathe, Kansas, USA).

Breeding behavior

To determine if breeding occurred in the population, and if so, which radio-tagged individuals bred, I observed radio-tagged and unbanded Clark's nutcrackers throughout the prebreeding, breeding and preharvest seasons. I documented nest building, nesting behavior, and if adults were seen in the company of fledglings [26]. If a radio-tagged individual did not exhibit any nest building or nesting behavior, and was not seen in the company of fledglings, I labeled it as nonbreeding. I documented all banded and unbanded fledglings observed at all times while in the field.

Statistical Analyses

Home range estimation

I collected prebreeding, breeding and preharvest location data on Clark's nutcrackers in 2011 and 2012. I calculated area-observation curves for prebreeding through preharvest 95% fixed kernel home ranges, and the curves for a subset of ten randomly chosen individuals (for which I had a minimum of 70 points, $n = 47$) at increments of 5, up to 70 points (5 points, 10 points, etc.) [22,30]. I selected points for the area-observation curves randomly [31]. Previous simulation studies found that 30-50 points randomly drawn from multiple known distributions were sufficient to accurately define home range [32,33]. Therefore, to be conservative, I defined an individual as being adequately sampled if I obtained 30 locations, though this conventional

cut-off was higher than the asymptote of the area-observation curves.

To minimize bias associated with autocorrelation, I did not use all relocation points when estimating an individual's home range [34]. However, elimination of autocorrelation (i.e. elimination of points) might alter the apparent habitat selection patterns of the birds and alter the utilization distribution (UD) [35]. Therefore, I determined biological rather than statistical independence of points [35,36]. Biological independence is defined as the temporal interval long enough to allow an individual to move from any point within its home range to any other point within its home range [36].

To determine which points to use, I first plotted the prebreeding through preharvest season 100% minimum convex polygon (MCP) of each individual with ≥30 points. These points included each locational point once per observation regardless of how long the bird stayed at the point, and only included individuals in the first year radio-tracked. With these data, I determined the median length (the longest distance between two boundaries) of a home range. To estimate the rate a bird could travel, I quantified the rate of movement (m per min) between consecutive points during all focal observations during which the bird was continuously tracked. The maximum speed I observed an individual flying was 48 km per hr, consistent with Vander Wall et al.'s [16] estimate of 45 km per hr. If flying 48 km per hr, an individual could cross the median length of a home range in four minutes; therefore, biological independence of points was achieved during this time [29,37]. For all analyses using "points" hereafter, unless stated otherwise, I used points which were separated by at least four minutes, including the same location more than once if the individual stayed at the location for ≥4 minutes. During the nesting period, I only included the point for the first observation made at the nest, to ensure home range size estimates were not biased due to repeated observations made at the nest [38].

I estimated the breeding season home range of each individual with ≥30 points during the breeding season. One bird was tracked in both 2011 and 2012; to avoid pseudoreplication, I did not include its 2012 range in analyses. To estimate the 95% and 100% MCP home ranges, I used the "adehabitatHR" package [39] in Program R (version 3.1.0, R Development Core Team). To estimate the 50%, 95% and 99% fixed kernel breeding season home ranges, I used the Geospatial Modeling Environment (version 0.7.2.1) software [32,40,41]. I used the 'plug-in' method for calculating the bandwidth parameter because of better convergence and reasonable tradeoffs between bias and variance compared to the commonly used reference and least squares methods [42–44]. One individual had a bimodal range: it regularly used one area, then moved to a distant, separate area, where it remained for the rest of the breeding season. For this individual, for each of the 50%, 95% and 99% fixed kernel methods, I calculated two separate home ranges. I then added the area of each pair of home ranges together. I present the 95% fixed kernel home range sizes which I use in analyses, as well as the 50% and 99% fixed kernel and 95% and 100% MCP home range sizes to compare my home range estimates to those of other studies.

I conducted Kendall's rank correlations to ensure that I had adequately sampled individual locations during the breeding season. There was no correlation between the 95% fixed kernel home range size and the number of points per individual (n = 55, tau = 0.12, P = 0.2), or the home range size and the number of days tracked (n = 55, tau = 0.05, P = 0.6) [33,45]. I used home range sizes calculated by the 95% fixed kernel method in all statistical analyses.

To compare home range size of 2011 nonbreeders and 2012 breeders, for each method of home range estimation, I square root transformed the estimated home ranges sizes, and used a t-test. I included only one randomly selected bird from each mated pair. Due to the low sample size (n = 3) of 2012 nonbreeders causing unbalanced sample sizes, I did not include 2012

1340 nonbreeders in these analyses.

1341 **Habitat selection**

1342 I constructed a geospatial layer of land cover types using map data from five vegetation
1343 maps (S3.1 Table). When discrepancies occurred, the layers were prioritized in the order listed. I
1344 classified habitat into ten categories (Table 3.1). The six whitebark pine health categories are
1345 those described in the whitebark pine stand-level condition assessment [46]. The ecologically-
1346 based categories were assigned based on spatial data on canopy damage and stand structure for
1347 use in prioritizing stands for protection and restoration [46]. The categories were stable through
1348 2011 and 2012 because, though low numbers of whitebark pines continued to die, the large-scale
1349 mountain pine beetle epidemic ended at the study area due to a cold-snap in early autumn 2009
1350 [47]. I radio-tracked and observed individuals foraging in all six available conifer habitats in the
1351 study area. When they foraged on seeds vs. alternative foods, I primarily observed Clark's
1352 nutcrackers foraging on whitebark pine, limber pine and Douglas-fir seeds. Therefore, each of
1353 these conifers was categorized separately from all other conifers. Non-conifer habitat was
1354 included as a separate category.

1355 **Table** 3.**1. Habitat categories.**

Habitat Categories	**Average % (± SEM) of available habitat on landscape (in and within 32 km of each home range)**
Whitebark pine, very low mortality, no to very low mountain pine beetle* activity	1.2 ± 0.1%
Whitebark pine, low mortality, low mountain pine beetle activity	1.8 ± 0.1%

Whitebark pine, moderate to high mortality, low to moderate mountain pine beetle activity	3.1 ± 0.2%
Whitebark pine, high mortality, very high mountain pine beetle activity	4.9 ± 0.4%
Whitebark pine, very high mortality, very low mountain pine beetle activity, all or most of whitebark pine overstory has died	0.1 ± 0.0%
Whitebark pine, burned	0.1 ± 0.0%
Limber pine	0.3 ± 0.0%
Douglas-fir	5.8 ± 0.2%
Other conifers (Engelmann spruce, lodgepole pine, and/or subalpine fir)	35.9 ± 0.5%
Non-conifer (may contain isolated trees, and isolated small stands)	47.0 ± 0.8%

* *Dendroctonus ponderosae*

I assessed Clark's nutcracker home range and within home range habitat selection with resource selection indices [48]. In the second-order selection [49], I compared the habitat within the home range of each bird with the available habitat on the landscape. Available habitat was defined as the habitat within the home range and within 32 km of each home range boundary. I designated the buffer as 32 km because previous research documented that Clark's nutcrackers will travel up to 32.6 km from their summer home range (which they assumed was equivalent to their breeding season home range) to harvest seeds [22]. In the third-order selection [49], I

compared the proportion of habitat used within the home range (based on habitat at GPS locations where each bird was observed) with the proportion of habitat available within their home range.

For each bird, I calculated second- and third-order selection ratios for each of the ten habitat categories (*i*) as w_i = (proportion used $habitat_i$)/(proportion available $habitat_i$). To calculate a resource selection index, I then standardized: median Manly beta index (b_i) = (selection $ratio_i$)/(sum of selection ratios for all habitat types) [50]. The standardized resource selection function is the probability that for any selection event, an individual would choose habitat *i* over all others, assuming all habitats are available in equal proportion.

For both second and third-order selection, I tested habitat selection using a chi-square for each bird, with a Design III analysis in the "adehabitatHS" package [39] in Program R. I tested if overall habitat selection for each group and for each individual were significantly different from random. For the tests of group selection, to meet the assumption of independence, I removed one randomly selected individual of each mated pair from the analyses (n = 3 in 2011, n = 8 in 2012). I then determined the Bonferroni 95% confidence intervals for population selection ratios for all birds in 2011 (all nonbreeding; n = 22) and breeding birds in 2012 (n = 19). Assumptions included independence between individuals, all individuals selected habitat in a similar way though as expected there was some variation, no territoriality, and all individuals had equal access to all available resource units. Using radio-tracking to detect locations of individuals circumvented the issue of imperfect detection.

Foraging behavior and diet

I classified each foraging event by the food type (e.g., invertebrates, seeds retrieved from cache, Douglas-fir seeds). Due to the size variation between seeds, it was possible to determine

that the seeds retrieved from caches were likely whitebark pine, and were not Douglas-fir; however, I was not able to exclude the possibility that some retrieved cached seeds were limber pine. However, limber pines in the study area were few and patchily distributed. Though they are an important late summer food source, the majority of seeds were eaten immediately rather than cached (T. D. Schaming personal observation).

I compared the proportion of the foraging observations composed of each food type between 2011 and 2012 using binomial tests. I then tested foraging habitat selection using a chi-square for each bird, with a Design III analysis in the "adehabitatHS" package [39] in Program R. I tested if overall foraging habitat selection for each group and for each individual were significantly different from random. For the tests of group selection, I removed one randomly selected individual of each mated pair from the analyses (n = 3 in 2011, n = 8 in 2012). I then determined the Bonferroni 95% confidence intervals for population selection ratios for all birds in 2011 (all nonbreeding; n = 22) and breeding birds in 2012 (n = 19). To assess if foraging habitat predicted food types eaten, I used a chi-square to determine if the food types composing >2.5% of the diet (excluding suet, which I used as bait for trapping, and unknown food types) were more likely to be eaten in specific habitats.

Other

I used R to perform all analyses, unless otherwise stated. I checked for normality and homogeneity of variance, applied $P \leq 0.05$ as the significance level, and reported means ± standard error.

Data

All of my original data from which this article is based are deposited at Figshare http://dx.doi.org/10.6084/m9.figshare.1439490. Four sets of habitat maps were obtained from

third parties and are available upon request. Data from the whitebark pine stand-level condition assessment are available from The Greater Yellowstone Whitebark Pine Subcommittee (contact the current committee chair listed on http://fedgycc.org/WhitebarkPineOverview.htm). The Bridger-Teton National Forest and Grand Teton National Park maps can be obtained from Nancy Bockino (Nancy_Bockino@nps.gov, Grand Teton National Park). The Shoshone National Forest maps can be obtained from Janice Wilson (janicewilson@fs.fed.us, U.S. Forest Service Rocky Mountain Region Regional Office, Geospatial Services). Wyoming GAP analysis vegetation maps are available online from the U.S. Geological Survey National Gap Analysis Program Land Cover Data Portal (http://gapanalysis.usgs.gov/gaplandcover/).

Results

Home Range Estimation

In 2011 and 2012, 83% (n = 29) and 74% (n = 34) of radio-tagged Clark's nutcrackers remained on the study area through the end of the breeding season (S3.2 Fig). A "missing" bird may have died, lost its antenna, permanently dispersed, or temporary emigrated (not returning to the study area until after the field season ended November 20, 2011 or October 31, 2012). I recorded adequate points to determine the breeding season home range for 55 Clark's nutcrackers (Table 3.2). Observations of radio-tagged birds occurred throughout the day between 0400 and 2400 hours standard time, with the heaviest sampling between 0800 and 1600 (S3.2 Table).

Table 3.2. The number of points recorded for and the number of separate days I followed individual Clark's nutcrackers.

	Prebreeding, breeding and seed	Breeding season only

	preharvest (combined)			
	2011	**2012**	**2011**	**2012**
Mean # of points ± SEM (range)	114 ± 9 (34 – 178)	98 ± 5 (30 – 135)	156 ± 12 (44 – 290)	116 ± 21 (31 – 207)
Mean # of days ± SEM (range)	18 ± 2 (7 – 32)	15 ± 1 (4 – 24)	10 ± 1 (3 – 15)	9 ± 1 (4 – 14)
# of birds	25	31	25	30

For the combined prebreeding, breeding and seed preharvest seasons, I include radio-tagged birds for which I recorded ≥30 points (one point per location). For the breeding season only, I include birds for which I had ≥30 independent breeding season points (≥4 minutes apart, multiple points per location possible).

Area-observation curves reached an asymptote with an average of 26 ± 4 points (n = 10), consistent with Lorenz and Sullivan's asymptote of 25 points for Clark's nutcracker summer ranges [22]. The median length of a 100% MCP prebreeding through preharvest season home range was 3,154 m (n = 56, mean = 3,955, range = 864 – 28,141 m). Mean breeding home range size of 2011 nonbreeders was significantly larger than the range size of 2012 breeders (t = 2.4, df = 36, P = 0.02; Table 3.3 and Fig. 3.2). Due to low sample size (n = 3), I did not include the 2012 nonbreeders in these analyses; however, 2012 nonbreeders' home range sizes were more similar to 2011 nonbreeders than to 2012 breeders (Fig. 3.2).

Table 3.3. Breeding season 95% fixed kernel home range sizes for breeding and nonbreeding birds.

Breeding status	**Mean home range size ± SEM (range; ha)**

	2011	2012
Breeder	NA	101 ± 23 (15 – 392); n = 19
Nonbreeder	214 ± 53 (3 – 1231); n = 22	202 ± 53 (116 – 297); n = 3

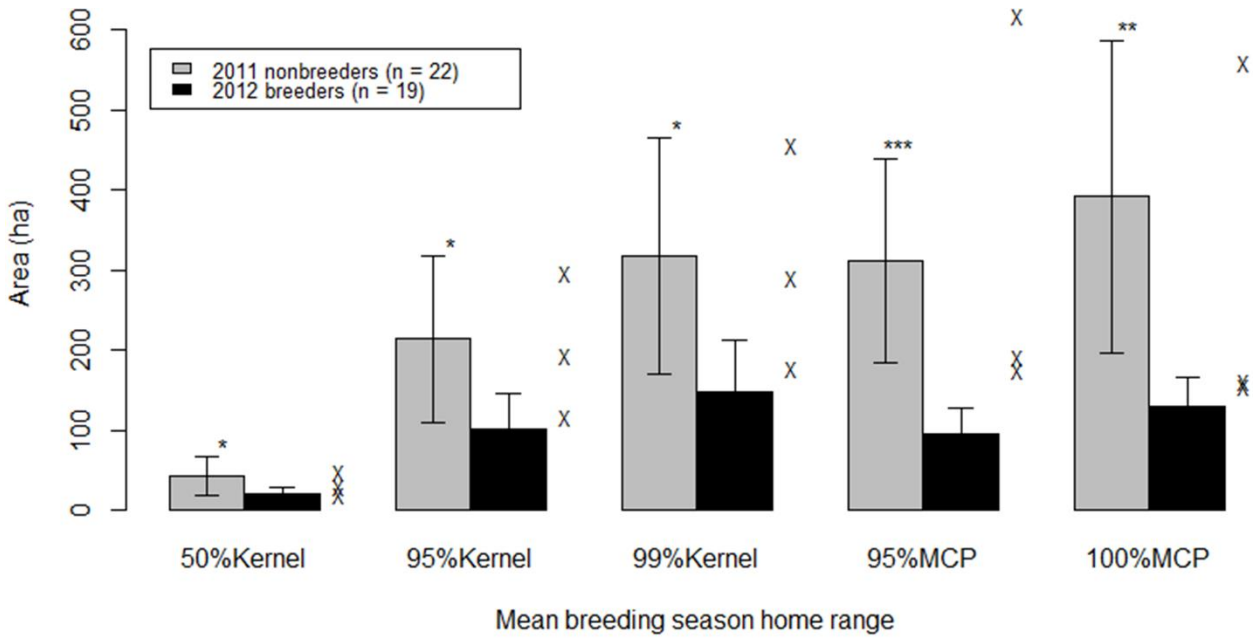


Figure 3.2. Estimated breeding season home range size. Estimated home range size of 2011 nonbreeders was significantly larger than range size of 2012 breeders. The estimated home range size for the three 2012 nonbreeders are included as X's on the graph, but due to low sample size, were not included in analyses.

Territoriality

The Clark's nutcracker territories overlapped considerably (S3.1 Text). I did not see any aggressive territorial interactions in 771.6 hours of observing radio-tagged birds in 2011 and 2012, or during numerous observations of other Clark's nutcrackers during 1,109 person-days in

the field (2009 – 2013). I also regularly observed all breeding and nonbreeding radio-tagged birds in flocks with >2 birds during every season.

Habitat Selection

Clark's nutcrackers in 2011 and breeding birds in 2012 did not select home range habitat randomly from within the available habitat on the landscape, or from within the home range (Table 3.4). In selecting home range habitat, Clark's nutcrackers in both 2011 and 2012 only selected Douglas-fir habitat in higher proportion than the proportion available (Fig. 3.3; S3.3 Table). They selected habitat without conifers in lower proportion than the proportion available, and never used whitebark pine with very low, low, or very high mortality, or burned whitebark pine. In selecting locations for all behaviors (e.g., foraging, flying, perching, breeding activity) from within the home range, Clark's nutcrackers only showed a slight positive selection for one habitat, other conifers, in 2012 (Fig. 3.4; S3.4 Table). All other available habitats were selected according to availability or in lower proportion than the proportion available. Limber pine's large confidence intervals were due to the variability of selection between individuals: 24% of the individuals selected limber pine, whereas 76% did not use limber pine at all.

Table 3.4. Home range and within home range habitat selection.

	Habitat selection			
	Home range vs. habitat available on landscape		**Locations of birds vs. habitat available in home range**	
	2011	**2012**	**2011**	**2012**
Random or nonrandom	Nonrandom	Nonrandom	Nonrandom	Nonrandom
$XL2^2$	16698967	9628923	507	348

df	59	53	45	44
P	< 0.001	< 0.001	< 0.001	< 0.001
# of birds	22	19	22	19
Fig.	3.3		3.4	

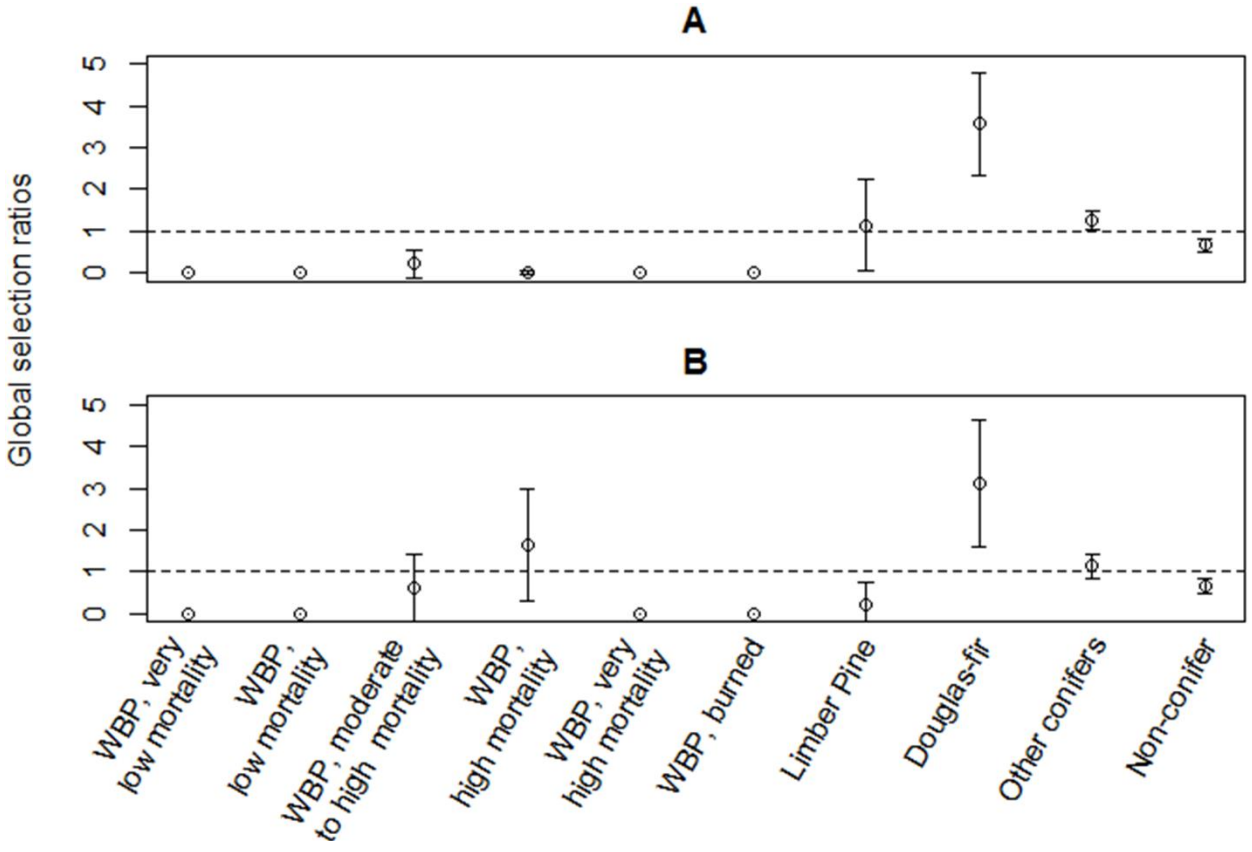


Fig. 3.3. Home range habitat selection. Clark's nutcracker selection of the home range habitat as compared to habitat available within 32 km in (**A**) 2011 (all nonbreeding birds) and (**B**) 2012 (breeding birds only). The Manly selectivity measure (± Bonferroni 95% confidence intervals (CI's)) was used to determine if habitats were used in higher proportion than the proportion available (>1), used in the same proportion as the proportion available (CI's include 1), used in

lower proportion than the proportion available (0<X<1) or never used (0). Whitebark pine is abbreviated as WBP.

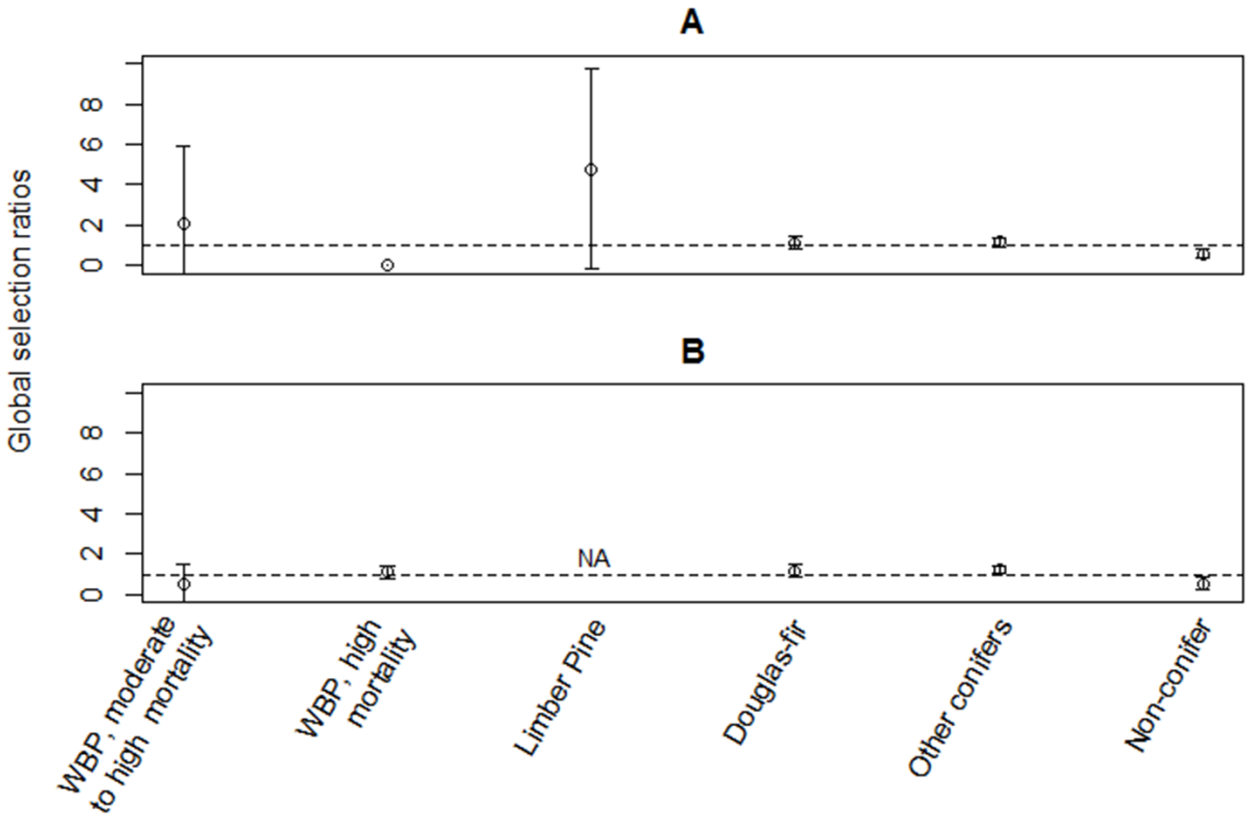


Fig. 3.4. Habitat selection within the home range. Clark's nutcracker selection of the habitat at locations from within the home range in (**A**) 2011, all nonbreeding birds and (**B**) 2012, breeding birds only. The Manly selectivity measure (± Bonferroni 95% confidence intervals (CI's)) was used to determine if habitats were used in higher proportion than the proportion available (>1), used in the same proportion as the proportion available (CI's include 1), used in lower proportion than the proportion available (0<X<1) or never used (0). Whitebark pine is abbreviated as WBP.

Foraging Behavior and Diet

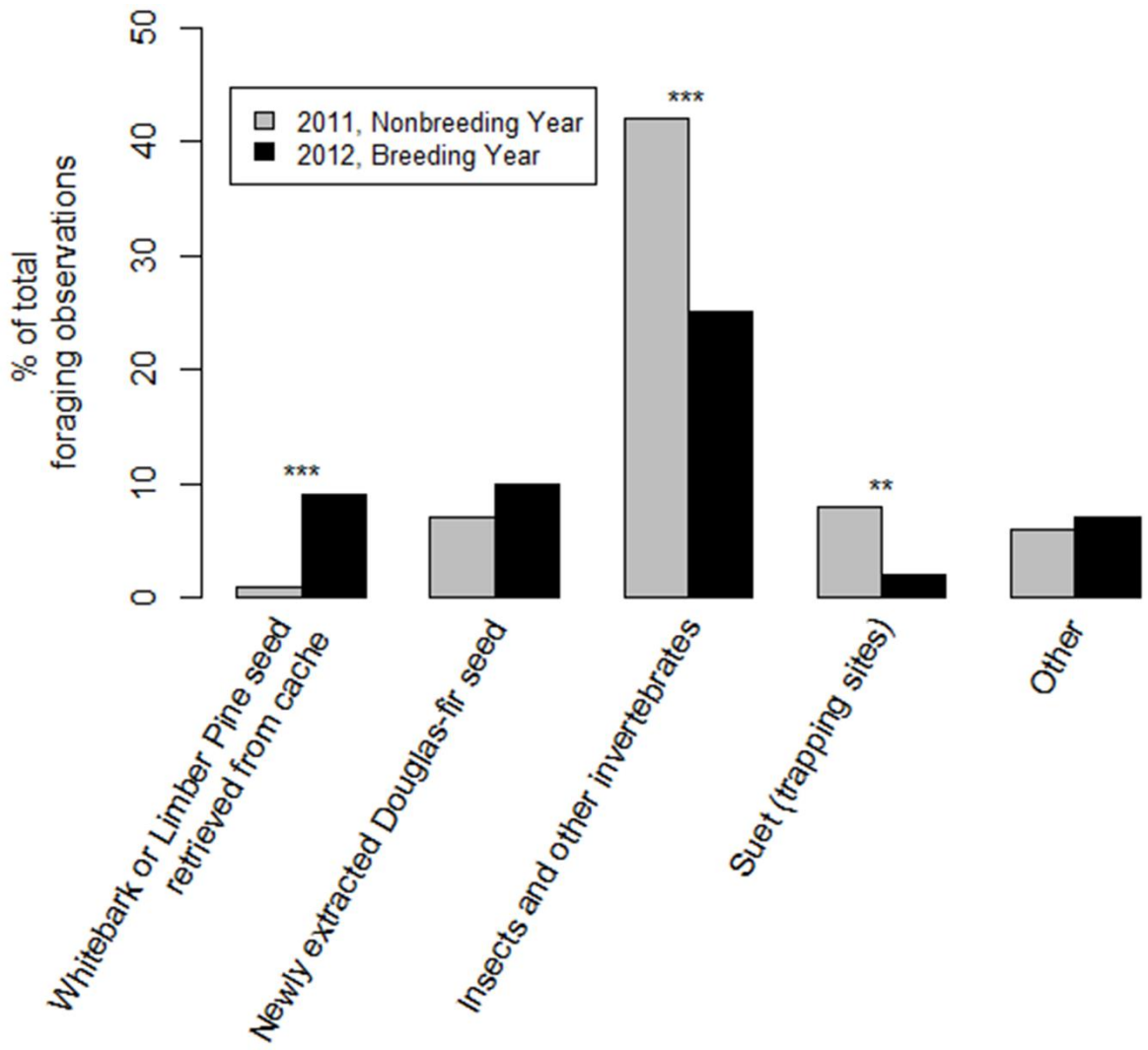
I observed foraging events of radio-tagged Clark's nutcrackers 358 and 293 times during the breeding season in 2011 and 2012, respectively (Table 3.5). On average, I observed foraging 14 ± 2 times per individual in 2011 (n = 26), and 9 ± 1 times per individual in 2012 (n = 33). Over the 103 day breeding season each year, I observed foraging on 57 days in 2011 and 54 days in 2012. On average, I observed foraging 6 ± 1 and 5 ± 1 times per day (with foraging observations) in 2011 and 2012, respectively.

Table 3.5. Food consumed during foraging events.

Food type	# of events (%)	
	2011	**2012**
Seed retrieved from cache	2 (1%)	26 (9%)
Invertebrates	152 (42%)	73 (25%)
Douglas-fir cone (on ground or in tree)	26 (7%)	28 (10%)
Suet (trapping sites)	30 (8%)	7 (2%)
Limber pine cone	1 (0.3%)	2 (1%)
Engelmann spruce cone	4 (1%)	6 (2%)
Lodgepole pine cone	8 (2%)	5 (2%)
Subalpine fir cone	0 (0%)	1 (0.3%)
Douglas-fir male cone	4 (1%)	0 (0%)
Lodgepole pine male cone	0 (0%)	2 (1%)
Douglas fir buds	1 (0.3%)	0 (0%)
Dead animal	3 (1%)	3 (1%)

Rodent (depredated)	0 (0%)	1 (0.3%)
Unknown – on ground	117 (33%)	120 (41%)
Unknown – in tree	10 (3%)	19 (6%)

I observed individuals eating significantly more invertebrates ($\chi^2 = 21.2$, df = 1, $P < 0.001$), and suet ($\chi^2 = 9.7$, df = 1, $P = 0.002$) in 2011, and significantly more seeds retrieved from caches ($\chi^2 = 25.1$, df = 1, $P < 0.001$) in 2012 (Fig. 3.5). Clark's nutcrackers foraged on similar proportions of newly extracted Douglas-fir seeds in both years ($\chi^2 = 0.8$, df = 1, $P = 0.4$). When the food type was undetermined, the majority of the time foraging occurred on the ground vs. in the trees. It is unlikely that there was a bias between years in the percentage of specific food types listed as unknown. When foraging, Clark's nutcrackers in 2011 and breeding Clark's nutcrackers in 2012 did not select foraging habitat at locations randomly from within the home range ($n = 25$, $XL2^2 = 83.9$, df = 39, $P < 0.001$, and $n = 27$, $XL2^2 = 57.4$, df = 32, $P = 0.004$, respectively; Table 3.6 and S3.5 Table).



1516

1517 **Fig. 3.5. Food types.** Percentage of known food types eaten during independent foraging events.

1518 Numbers do not add up to 100, as foods consumed during <2.5% of the events, and unknown

1519 food items are not included in the graph.

1520

1521 **Table 3.6. Clark's nutcracker foraging habitat selection from within the home range.**

Habitat	Food type			
	All	**Invertebrates**	**Douglas-fir seeds**	**Seed caches**

	2011	2012	2011	2012	2011	2012	2012
Whitebark pine, moderate to high mortality	0	0	0	0	0	0	0
Whitebark pine, high mortality	0	+	0	=	0	0	=
Limber pine	=	NA	=	NA	0	NA	NA
Douglas-fir	=	=	=	=	=	=	=
Other conifers	=	=	=	=	=	=	=
Non-conifer	=	=	=	-	=	=	=

The habitat within the home range was considered the available habitat, and the habitat where foraging events occurred was considered used habitat. "+" = habitat used in higher proportion than the proportion available; "=" = habitat used in the same proportion as the proportion available; "-" = habitat used in lower proportion than the proportion available; "0" = habitat never used; "NA" = habitat was not available within home ranges. Habitat selection for foraging on seed caches was not included for 2011 as I only observed two events.

Discussion

Habitat Selection

These results suggest that, at my study site in the Greater Yellowstone Ecosystem, Douglas-fir habitat is the most important breeding season habitat for Clark's nutcrackers. Clark's nutcrackers selected Douglas-fir habitat in two years with contrasting food availability and breeding status. This selection occurred following a low whitebark pine cone crop, when population-wide nonbreeding occurred, and birds could therefore range more widely to track

ephemeral food sources. It also occurred following a high whitebark pine cone crop when the majority of birds bred and were constrained to a nest site. It is unlikely that individuals were excluded from high quality habitat due to territoriality, because I did not observe territorial behavior, and home ranges overlapped extensively. Previous observational research had documented Clark's nutcrackers using Douglas-fir habitat during the breeding season [11,51]. However, this is the first systematic study of space use of radio-tracked Clark's nutcrackers to document breeding season selection of Douglas-fir habitat.

Clark's nutcrackers specialize on large seeded pines, which are the whitebark pines and limber pines in the Greater Yellowstone Ecosystem [9,10]. I observed the majority of the radio-tagged Clark's nutcrackers eating whitebark pine seeds between July and September in both 2011 and 2012 (T. D. Schaming personal observation). However, for their breeding season home range, the birds did not select either healthy or degraded whitebark pine, or limber pine habitats. This finding supports previous observations of infrequent use of whitebark pine communities during the breeding season [See 6]. For example, Tomback [17] observed that after whitebark pine cone crops were depleted, Clark's nutcrackers in the Sierra Nevada migrated to lower elevations, where they stayed for the winter and spring breeding season. In contrast, in the only previous formal study of space use of individually marked Clark's nutcrackers, Lorenz [27] determined that resident summer ranges contained proportionately more parkland whitebark pine (whitebark pine dominated, <10% canopy cover) and mixed forest compared to availability. Though she did not evaluate breeding season range separately, due to caching locations, she inferred that the summer range was also the winter and spring breeding season range.

Though Clark's nutcrackers did not positively select moderate to high and high mortality whitebark pine habitats, selection did vary for those habitats. In 2012, the year following a high

1559 whitebark pine cone crop, Clark's nutcrackers selected the two habitats in proportion to
1560 availability. In contrast, in 2011, the year following a low whitebark pine cone crop, they
1561 selected those habitats less than expected compared to availability. It is reasonable that Clark's
1562 nutcrackers would use whitebark pine habitats less after a low whitebark pine crop, because a
1563 lower cone crop likely translates to fewer cached seeds. Though Clark's nutcrackers transport
1564 their seeds up to 32.6 km, they also regularly cache seeds close to the parent trees [17,52]. The
1565 high spring snowpack in 2011, as compared to 2012, may have also contributed to the lower
1566 selection of the high elevation whitebark pine habitats in 2011. Overall, snow melted faster at
1567 lower elevations (T. D. Schaming personal observation). The finding that Clark's nutcrackers
1568 adjusted their breeding season selection of whitebark pine habitat between years suggests that, in
1569 some years, even though it is not positively selected, whitebark pine habitat may be used more
1570 than previously expected during the spring breeding season.

1571 Clark's nutcrackers may have selected Douglas-fir because of its low elevation, milder
1572 winter conditions; however, limber pine and other conifer habitats (Engelmann spruce, lodgepole
1573 pine, and/or subalpine fir) were also located at lower elevations. The birds only used limber pine
1574 habitat in the proportion available in 2011, and used it less than available in 2012. Clark's
1575 nutcrackers did select other conifer habitat following a low whitebark pine cone crop, but the
1576 selection was weak. These results suggest that for their breeding season home range, Clark's
1577 nutcrackers are specifically selecting habitat with an available seed source, rather than just
1578 milder winter conditions.

1579 Though it is only a sample size of two years, this variation in selection suggests that
1580 Clark's nutcrackers alter their space use depending on demographic and/or environmental
1581 conditions, such as breeding condition or whitebark pine cone crop. Understanding the variation

in size of home range and habitats selected in different years aids managers in determining the amount and diversity of habitats necessary for Clark's nutcrackers to persist in an ecosystem.

Foraging Behavior and Diet

When foraging within the home range, Clark's nutcrackers selected high mortality whitebark pine habitat in 2012 in higher proportion than available. Given that past research has documented seed caching near parent trees [12], it is unsurprising that individuals are more likely to select some whitebark pine habitats for foraging in years following a large cone crop. The birds consistently selected Douglas-fir, other conifer and non-conifer habitat in proportion to availability both years. When specifically foraging for the three most common food sources (>2% of identified foraging events), invertebrates, Douglas-fir seeds and seed caches, they showed no positive selection for a specific habitat. Though Clark's nutcrackers specialize on large seeded pines, they are opportunistic foragers [6]. Due to their varied diet, it is reasonable that the birds forage when the opportunity arises (e.g. dead animal, suet), regardless of the habitat.

Though they did not select Douglas-fir habitat for foraging disproportionate to availability, the Clark's nutcrackers selected Douglas-fir habitat for the home range. Hence, availability of Douglas-fir habitat was already higher than expected within the home range. Therefore, foraging in Douglas-fir in proportion to availability shows strong selection of Douglas-fir habitat. The stability of selection of Douglas-fir habitat across years with variable demographic and environmental conditions validates its importance as foraging habitat. On the other hand, the Douglas-fir cone crop was high each year, 2008-2014 (T. D. Schaming personal observation); therefore, it is unclear how Clark's nutcracker habitat selection would change in years with a low Douglas-fir cone crop.

Both years, I observed individuals foraging on newly extracted Douglas-fir seeds in Douglas-fir, other conifer and non-conifer habitats. Douglas-fir seeds were therefore available in multiple habitats, not just the habitat dominated by Douglas-fir stands. Foraging on Douglas-fir in all three habitat types emphasizes the importance of Douglas-fir as a food source. The inclusion of Douglas-fir seeds in the spring diet was previously documented by Giuntoli and Mewaldt's [23] analysis of Clark's nutcracker stomach contents. However, it is unclear whether the seeds were newly harvested or cached the previous autumn. Clark's nutcrackers have been observed to eat seeds which remained in cones through the spring: Tomback documented Clark's nutcrackers feeding on Jeffrey pine cones during the breeding season [53]. Habitats which contain seeds remaining available through the spring may be particularly important for Clark's nutcrackers in locations with declining whitebark pine ecosystems.

In contrast to the stability of the importance of Douglas-fir seeds, I observed Clark's nutcrackers foraging on few seed caches, even after a high whitebark pine cone crop (S3.2 Text). Though it is possible that some of the unknown foraging events included seed caches, it is unlikely that I was unable to detect seed cache retrieval in most situations. Past research documented Clark's nutcrackers eating and feeding nestlings cached seeds in the spring [11,23,53]. However, my results suggest that the importance of cached seeds in the breeding season diet may be overestimated. Alternatively, it may be highly variable between regions. Even in 2012, seed caches accounted for only 9% of the breeding season foraging events. Douglas-fir cones accounted for a similar 10%, while invertebrates were eaten in approximately three times the number of foraging events (42% in 2011; 25% in 2012). Similarly, previous research found that during the breeding season, 44 – 100% of Clark's nutcracker stomach contents contained arthropods [23]. Invertebrates may be a more important part of the breeding

season diet, at least in some areas, than previous research suggested [11].

Conservation Implications

Whitebark pines are declining in the Greater Yellowstone Ecosystem [13,54]. Land managers have focused on restoring whitebark pine habitat, with the assumption that Clark's nutcrackers will be available to resume seed dispersal [21]. They presume the birds will disperse seeds once the whitebark pine forests reach an adequate state of health [21]. This, however, assumes that Clark's nutcrackers will persist in, or move back into locations once whitebark pine habitats are restored.

The Clark's nutcracker is a partially migratory, irruptive seed specialist [16]. Dohms and Burg [55] suggested there are high levels of gene flow among populations, unrestricted by potential barriers such as mountain ranges. Therefore, it is possible that Clark's nutcrackers may decline or become extinct locally, but could then recolonize an area once habitat improves, providing they survive elsewhere. However, given the widespread nature of the decline of five-needle pines, the best management practice may be to ensure a stable population of Clark's nutcrackers persists in the ecosystem.

It is important to consider which measures could maintain viable Clark's nutcracker populations. Lorenz suggested that increasing the health of ponderosa pine stands in her study area in the Cascade Range may sustain Clark's nutcracker populations during whitebark pine recovery [27]. This seems straightforward, as every individual in her study harvested and cached ponderosa pine seeds in the autumn. Even when whitebark pine seeds were available, not all birds harvested whitebark pine seeds. Unlike ponderosa pine, Douglas-fir are unlikely to replace whitebark pine in the diet due to their lower nutritional value and longer handling time [26]. Nevertheless, in my study area, Clark's nutcrackers selected Douglas-fir for their breeding

season home range. This selection has important implications for habitat conservation planning. Though they may not be able to persist solely on Douglas-fir seeds, the foraging provided by Douglas-fir stands may provide a critical alternative seed source in the Greater Yellowstone Ecosystem, helping the Clark's nutcrackers to meet their foraging requirements.

To my knowledge, whitebark pine restoration strategies focus nearly exclusively on whitebark pine forests. Managers do not account for the mobility of Clark's nutcracker populations. Instead of managing whitebark pine in isolation, they may need to consider the different habitats Clark's nutcrackers use throughout the year, as well as the variability of those habitats in years with differing demographic and environmental conditions.

The results of this study may be more representative of Clark's nutcracker behavior in degraded whitebark pine habitat, rather than healthy forest communities. However, the importance of alternative seed sources, such as Douglas-fir, may be particularly critical in these degraded habitats. With the widespread decline of their primary food sources, five-needle white pines, and in particular whitebark pine, habitats with alternative food sources may be increasingly important for supporting Clark's nutcracker populations. Due to the reduction in primary habitat, these habitats may offer refugia and may be critical for long-term population viability [56,57]. Optimizing landscape level management of whitebark pine restoration may be critical to conserving whitebark pine communities in the Greater Yellowstone Ecosystem. I specifically suggest that managers consider restoration locations adjacent to a mosaic of habitats which specifically includes Douglas-fir. By extrapolation, whitebark pine restoration efforts in other regions may consider prioritizing restoration of whitebark pine stands near alternative seed sources.

Managing wide-ranging species that require seasonally distinct and spatially discrete

habitats can be challenging [58]. Nevertheless, traditional approaches of focusing on protection of primary habitat may need to be reassessed in the face of a changing climate and widespread habitat decline [59]. Despite the constraints, policy makers may need to consider protecting broader areas to encompass all the resource requirements of populations [60].

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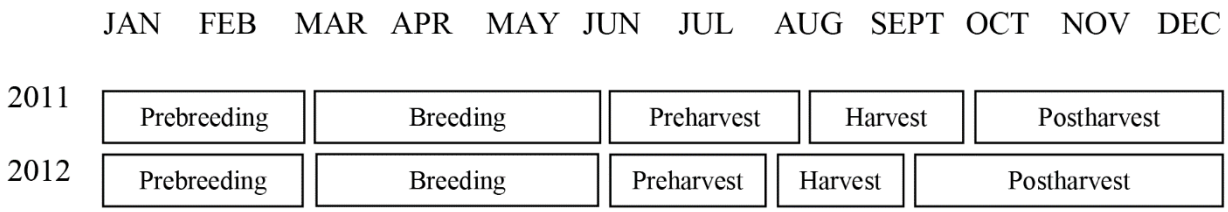
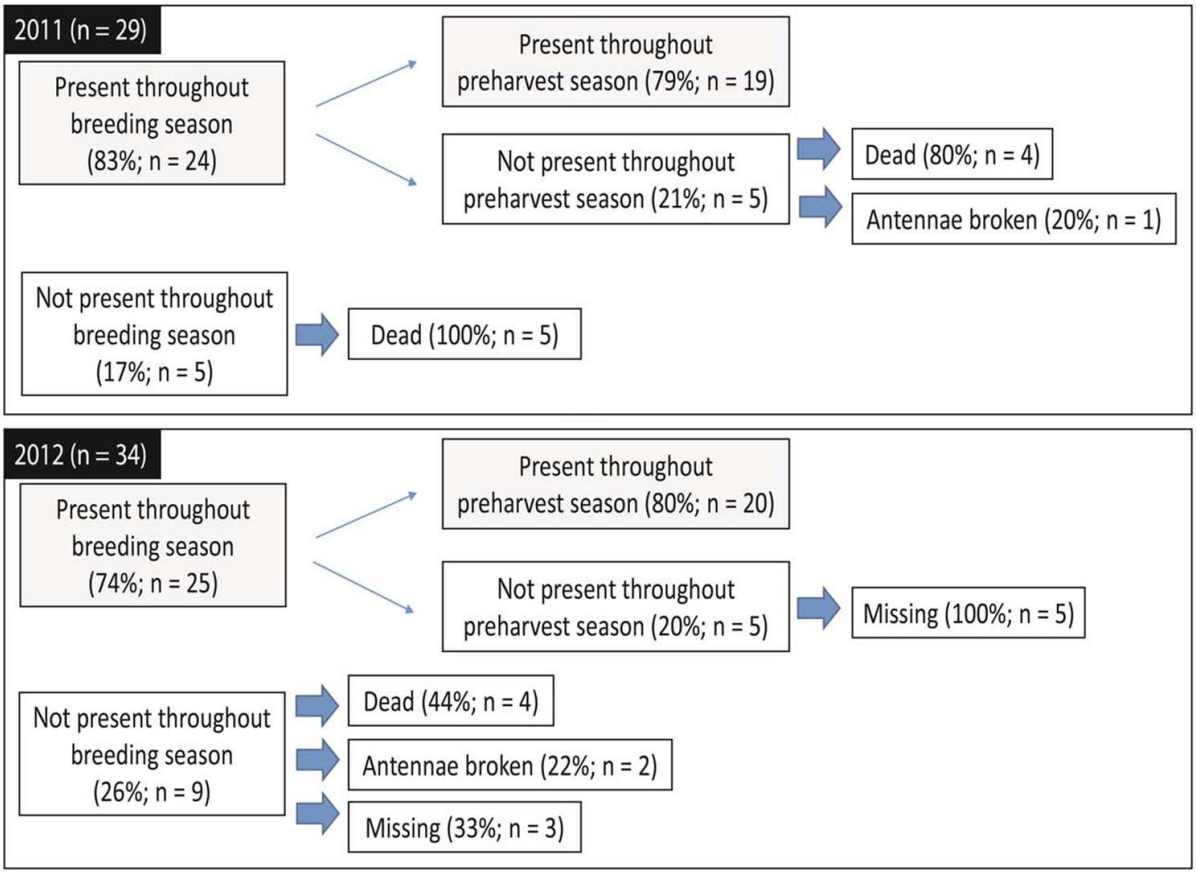
Supporting Information

S3.1 Figure. Timeline of Clark's nutcracker annual cycle in 2011 and 2012. (The focus of this study is on the breeding season.)



S3.2 Figure. Fate of radio-tagged Clark's nutcrackers during breeding and preharvest seasons.



S3.1 Table. Vegetation maps used to create the geospatial layer of land cover types.

Vegetation map data	Name of data file	Obtained from
Whitebark pine stand-level condition assessment	[1]	The Greater Yellowstone Whitebark Pine Subcommittee
Bridger-Teton National Forest	existveg_2007, USDA National Forest Service Remote Sensing Applications Center	Grand Teton National Park
Shoshone National Forest	FSVeg Spatial database, extracted March 22, 2012	U.S. Forest Service Rocky Mountain Region (R2) Regional Office, Geospatial Services
Grand Teton National Park	2005 vegetation mapping report	Grand Teton National Park
Wyoming GAP analysis	[2]	Online

References (S3.1 Table)

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S3.2 Table. Time of day during which I observed radio-tagged Clark's nutcrackers.

Time	2011	2012
0400-0600	1%	0%
0600-0800	4%	1%
0800-1000	21%	14%
1000-1200	29%	28%
1200-1400	26%	34%
1400-1600	18%	21%
1600-1800	2%	1%
1800-2000	0.4%	0%
2000-2200	0.4%	0%
2200-2400	0.05%	0%

S3.3 Table. The Manly selectivity measure (± Bonferroni 95% confidence intervals (CI's)) used to evaluate Clark's nutcracker selection of the home range habitat as compared to habitat available within 32 km.

Year	2011				2012			
Habitat	w_i	SEM	CI (low)	CI (high)	w_i	SEM	CI (low)	CI (high)
Whitebark pine, very low mortality	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Whitebark pine, low mortality	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Whitebark pine, moderate to high mortality	0.22	0.12	-0.13	0.56	0.61	0.29	-0.21	1.43
Whitebark pine, high mortality	0.01	0.01	-0.02	0.04	1.64	0.48	0.29	2.99
Whitebark pine, very high mortality	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Whitebark pine, burned	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Limber pine	1.14	0.39	0.05	2.23	0.21	0.20	-0.34	0.76
Douglas-fir	3.57	0.44	2.35	4.80	3.11	0.54	1.59	4.62
Other conifers	1.25	0.08	1.04	1.47	1.13	0.11	0.83	1.43
Non-conifer	0.67	0.06	0.51	0.83	0.66	0.06	0.49	0.83

S3.4 Table. The Manly selectivity measure (± Bonferroni 95% confidence intervals (CI's)) used to evaluate Clark's nutcracker selection of the habitat at locations from within the home range.

Year	2011				2012			
Habitat	w_i	SEM	CI (low)	CI (high)	w_i	SEM	CI (low)	CI (high)
Whitebark pine, moderate to high mortality	2.04	1.46	-1.80	5.88	0.53	0.37	-0.44	1.50
Whitebark pine, high mortality	0.00	0.00	0.00	0.00	1.10	0.13	0.76	1.44
Limber pine	4.77	1.88	-0.18	9.72	NA	NA	NA	NA
Douglas-fir	1.14	0.10	0.88	1.41	1.15	0.12	0.84	1.47
Other conifers	1.14	0.08	0.94	1.35	1.23	0.06	1.06	1.40
Non-conifer	0.59	0.08	0.37	0.82	0.55	0.11	0.26	0.84

1868 **S3.5 Table. The Manly selectivity measure (± Bonferroni 95% confidence intervals (CI's)) used to evaluate Clark's nutcracker**

1869 **selection of foraging habitat.**

1870

Habitat	w_i ± SEM (CI)						
	All Food		Invertebrates		Douglas-fir seeds		Seed caches
	2011	2012	2011	2012	2011	2012	2012
Whitebark pine, moderate to high mortality	never used	never used	never used	never used	never used	never used	never used
Whitebark pine, high mortality	never used	1.2 ± 0.06 (1.04-1.36)	never used	1.54 ± 0.35 (0.67-2.42)	never used	never used	0.53 ± 0.48 (-0.66-1.72)
Limber pine	4.9 ± 2.14 (-0.45-10.24)	NA	5.15 ± 3.49 (-3.57-13.86)	NA	never used	NA	NA
Douglas-fir	0.92 ± 0.11 (0.64-1.19)	1.27 ± 0.21 (0.74-1.8)	1.02 ± 0.18 (0.58-1.47)	0.84 ± 0.27 (0.17-1.51)	1.25 ± 0.26 (0.62-1.88)	0.84 ± 0.3 (0.12-1.56)	1.2 ± 0.56 (-0.19-2.59)
Other conifers	1.28 ± 0.12 (0.97-1.58)	1.04 ± 0.12 (0.75-1.33)	1.21 ± 0.11 (0.93-1.49)	1.34 ± 0.43 (0.27-2.4)	1.19 ± 0.51 (-0.04-2.42)	1.1 ± 0.2 (0.61-1.58)	1.16 ± 0.24 (0.55-1.77)

Non-conifer	0.67 ± 0.18 (0.22-1.11)	0.68 ± 0.17 (0.25-1.1)	0.64 ± 0.17 (0.21-1.08)	0.56 ± 0.17 (0.13-1)	0.57 ± 0.39 (-0.36-1.49)	1.01 ± 0.48 (-0.14-2.16)	0.8 ± 0.37 (-0.13-1.73)

1871

S3.1 Text. Home range overlap.

I calculated the overlap of each bird's breeding season home range with every other individual's home range by superimposing each pair of two-dimensional kernels [1]. Then, I used a Mann-Whitney-Wilcoxon Test to compare the mean overlap between mates vs. the mean overlap between unmated individuals. One individual had adequate locational points to determine the breeding season home range in both 2011 and 2012. I calculated the overlap between each year's home range to evaluate consistency of home range location between years.

Overlap of home range by mated pairs did not significantly differ from overlap of each individual with other individuals (excluding the individual's mate; $n = 77$, $W = 603$, $P = 0.99$; Table S3.1.1). Territories overlapped a mean of 10 ± 0 (median = 11) and 7 ± 1 (median = 8) other radio-tagged individuals in 2011 and 2012, respectively. This demonstrates extensive overlap. However, it is not reasonable to compare differences between years because not all individuals at a site were radio-tagged. All radio-tagged birds' ranges were also overlapped by unbanded birds. The one bird regularly radio-tracked both years retained use of 51% of its 2011 breeding range in 2012.

Table S3.1.1. Overlap of breeding season home ranges.

	Home range overlap			
	Mated pairs		**All individuals (excluding mate)***	
	2011	**2012**	**2011**	**2012**
Mean ± SEM	76 ± 4%	75 ± 4%	68 ± 6%	68 ± 6%
Median	71%	74%	73%	79%
Range	66 – 91%	50 – 98%	2 – 100%	0 – 100%
# of birds	6 (3 mated	16 (8 mated	25	30

	pairs)	pairs)		

*Overlap of home range by each individual with other radio-tagged individuals excluding the mate.

References (S3.1 Text)

1. White GC and Garrott RA. Analysis of Wildlife Radio-tracking Data. San Diego, CA, USA: Academic Press; 1990.

S3.2 Text. Variation in foraging on seed caches between years.

Clark's nutcrackers foraged on a significantly lower proportion of cached seeds in 2011, the year after a low whitebark pine cone crop. Foraging on fewer caches may have occurred because it was more difficult to access caches below the deeper snow pack in 2011. However, Clark's nutcrackers cache up to 59% of seeds aboveground [1], and regularly cache in exposed areas, such as steep cliffs and south facing slopes, where wind and sun prevent heavy snow accumulation [2–4]. The birds also retrieve caches from under the snow and ice [5]. I have seen a Clark's nutcracker dig diagonally down through the snow, until its body was completely buried, then return to the surface with whitebark pine seeds (recognizable by the size; T. D. Schaming personal observation). Hutchins saw an individual peck through eight inches of ice to pull out seeds (H. E. Hutchins personal observation).

References (S3.2 Text)

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CHAPTER 4

CLARK'S NUTCRACKER OCCURRENCE IN A REGION WITH WHITEBARK PINE DECLINE: IMPLICATIONS FOR CONSERVATION OF THE MUTUALISM[3]

Abstract

Mutualistic relationships between plants and their animal seed dispersers can begin to break down when habitat declines. Evidence suggests Clark's nutcracker (*Nucifraga columbiana*) populations are declining, and because whitebark pine (*Pinus albicaulis*) is an obligate mutualist of the bird, a decline in Clark's nutcracker populations would accelerate the disappearance of whitebark pines. This positive feedback loop could lead to mutualism breakdown. Our primary goal was to determine which habitat characteristics best predicted Clark's nutcracker occurrence - whitebark pine cone crop, or whitebark pine or Douglas-fir (*Pseudotsuga menziesii*) habitat at local and landscape scales. Between 2009 and 2013, we carried out 3,135 audio-visual Clark's nutcracker surveys at 238 random points in the southern Greater Yellowstone Ecosystem. Using Bayesian occupancy models and cross-product model selection, we evaluated the association between Clark's nutcracker occurrence and habitat variables during five stages of the annual cycle, while accounting for imperfect detection. Results suggest that Clark's nutcracker occurrence is positively associated with both the presence of cone-bearing whitebark pine trees and the area of whitebark pine on the landscape. To promote a high, >75%, probability of occurrence, we recommend a management plan that

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achieves a landscape composed of a minimum of 8% cone-bearing whitebark pine habitat (~25,000 ha) within a 32.6 km radius, rather than attempting to achieve a specific cone and basal area density within a stand. Additionally, an optimal habitat mosaic includes moderate levels of Douglas-fir habitat. Models currently used to guide whitebark pine management strategies underpredicted Clark's nutcracker occurrence in our study, suggesting these strategies are not appropriate in the Greater Yellowstone Ecosystem. The Clark's nutcracker-whitebark pine mutualism appears to be functional in the region. However, without knowledge of historical habitat use, we cannot predict how the relationship will change as the population density of each species changes. We therefore suggest adopting an adaptive monitoring approach and continuing to monitor the relationship as the environment changes and management strategies are implemented. Due to the high mobility of Clark's nutcrackers, we also suggest monitoring the status of the Clark's nutcracker metapopulation to allow for more robust predictions of stability of this keystone mutualism.

Key words

Clark's nutcracker, Greater Yellowstone Ecosystem, habitat loss, landscape, mutualism breakdown, mutualism stability, *Nucifraga columbiana*, occupancy, *Pinus albicaulis*, whitebark pine

Introduction

Habitat loss can have significant detrimental effects on forest community dynamics and persistence. In particular, mutualistic relationships between plants and their animal seed dispersers can begin to break down [1]. Mutualism abandonment, when one or both partners survive, but they cease to interact, may be particularly common in nutritional mutualisms when

one partner is facultative and can therefore acquire food from other local or regional sources [2]. The problem is: when the plant mutualists are obligate and cannot survive without their partner, they are especially vulnerable to extinction if their partner ceases to interact cooperatively [See 2]. Although mutualism breakdown is rarely documented [2,3], recent research supports the idea that habitat loss and fragmentation can disrupt mutualisms between plants and their seed dispersers [1,4,5]. To evaluate likelihood of mutualism breakdown in an ecosystem experiencing habitat loss, a first step is to determine if a species will continue to use an altered habitat, and hence be available to perform their ecosystem function (e.g. disperse seeds).

Clark's nutcrackers (*Nucifraga columbiana*) disperse seeds of at least ten species of conifers in the western U.S. [See 6]. They rapidly and effectively move seeds up to 32.6 km, across latitudinal and elevational gradients, and into disturbed areas [7,8]. The continued association between Clark's nutcrackers and conifers may be critical in maintaining healthy forests in the western U.S., and enabling rapid colonization of newly available ideal habitats. Whitebark pine (*Pinus albicaulis*), a candidate for the endangered species list, is an obligate mutualist of Clark's nutcrackers [9,10]. Therefore, it is particularly important that Clark's nutcrackers continue to disperse seeds within whitebark pine habitats. However, evidence suggests that Clark's nutcracker populations are declining in large parts of their range, likely as a result of the widespread decline of five-needle white pines [7,11,12]. The birds are still relatively common in the Greater Yellowstone Ecosystem, despite the high mortality of whitebark pines in the region [13,14]. Previous research suggests that Douglas-fir (*Pseudotsuga menziesii*) is an important alternative seed source when whitebark pine cone crops are low, and during the breeding season, radio-tagged Clark's nutcrackers selected Douglas-fir habitat [15,16]. We predicted that, because of the apparent dependence of Clark's nutcracker on both species,

1986 occurrence (use) patterns would be primarily influenced by both whitebark pine and Douglas-fir
1987 habitat.

1988 Extensive whitebark pine restoration efforts are underway, assuming that once a certain
1989 level of whitebark pine restoration has been achieved, Clark's nutcrackers will be available to
1990 continue dispersing seeds [17,18]. Understanding which habitat characteristics, and at what
1991 scale, increases the probability of Clark's nutcracker occurrence will aid in increasing the
1992 probability of the birds being locally available and help reduce the potentially detrimental impact
1993 of whitebark pine decline. Moreover, quantifying local thresholds of Clark's nutcracker
1994 occurrence will illuminate whether the current whitebark pine restoration guidelines are accurate
1995 for the Greater Yellowstone Ecosystem. The primary goal of this study was to determine whether
1996 presence or density of whitebark pine cone crop, presence or density of whitebark pine and
1997 Douglas-fir habitat at the local scale, and/or area of whitebark pine and Douglas-fir habitat at the
1998 landscape scale, best predicted Clark's nutcracker occurrence. Because Clark's nutcracker
1999 behavior varied considerably throughout the year, we analyzed occurrence separately for each of
2000 five stages of the birds' annual cycle: breeding season, early and late summer, fall seed harvest,
2001 and post-harvest, and quantified the threshold values of whitebark pine habitat above which
2002 Clark's nutcrackers had a high (>75%) probability of occurrence in each stage of the annual
2003 cycle. To inform current management strategies, we assessed whether previous studies
2004 accurately predicted our observation data from the southern Greater Yellowstone Ecosystem. To
2005 aid in the design of future Clark's nutcracker surveys, we compared how inference about
2006 occurrence patterns changed using alternative (<100, infinite) survey radii. Because we expected
2007 whitebark pine cone crop to be a strong predictor of occurrence, and because determining cone
2008 count is labor intensive, we also evaluated if it was possible to predict cone crop at a location

based on other habitat variables.

Materials and methods

Ethics statement

This research was approved by the Cornell University Institutional Animal Care and Use Committee (protocol # 2008-0176). We conducted all field work under U.S. Forest Service Special-Use Authorization # JAC747002 (2009-2013) and Grand Teton National Park Scientific Research and Collecting Permit #'s GRTE-2011-SCI-0052 and GRTE-2012-SCI-0069.

Field methodology

Study area

This study is based on five years (2009 - 2013) of Clark's nutcracker surveys carried out in the Greater Yellowstone Ecosystem, in northwestern Wyoming, primarily in Bridger Teton and Shoshone National Forests, and Grand Teton National Park (25,050 km^2; bounded by 45º00'01" N north, 42º09'14" N south, 111º02'56"W west, and 108º42'55"W east; Fig. 4.1). We conducted 3,135 point counts at 238 random sites. Sites ranged in elevation from 1,843 to 3,372 m, and were located in a habitat mosaic dominated by six conifer species, whitebark pine, Douglas-fir, limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea englemannii*), and subalpine fir (*Abies lasiocarpa*). The conifer habitat was interspersed with aspen (*Populus tremuloides),* sagebrush (*Artemesia tridentata*), grassy open areas, high mountain meadows and rocky outcroppings.

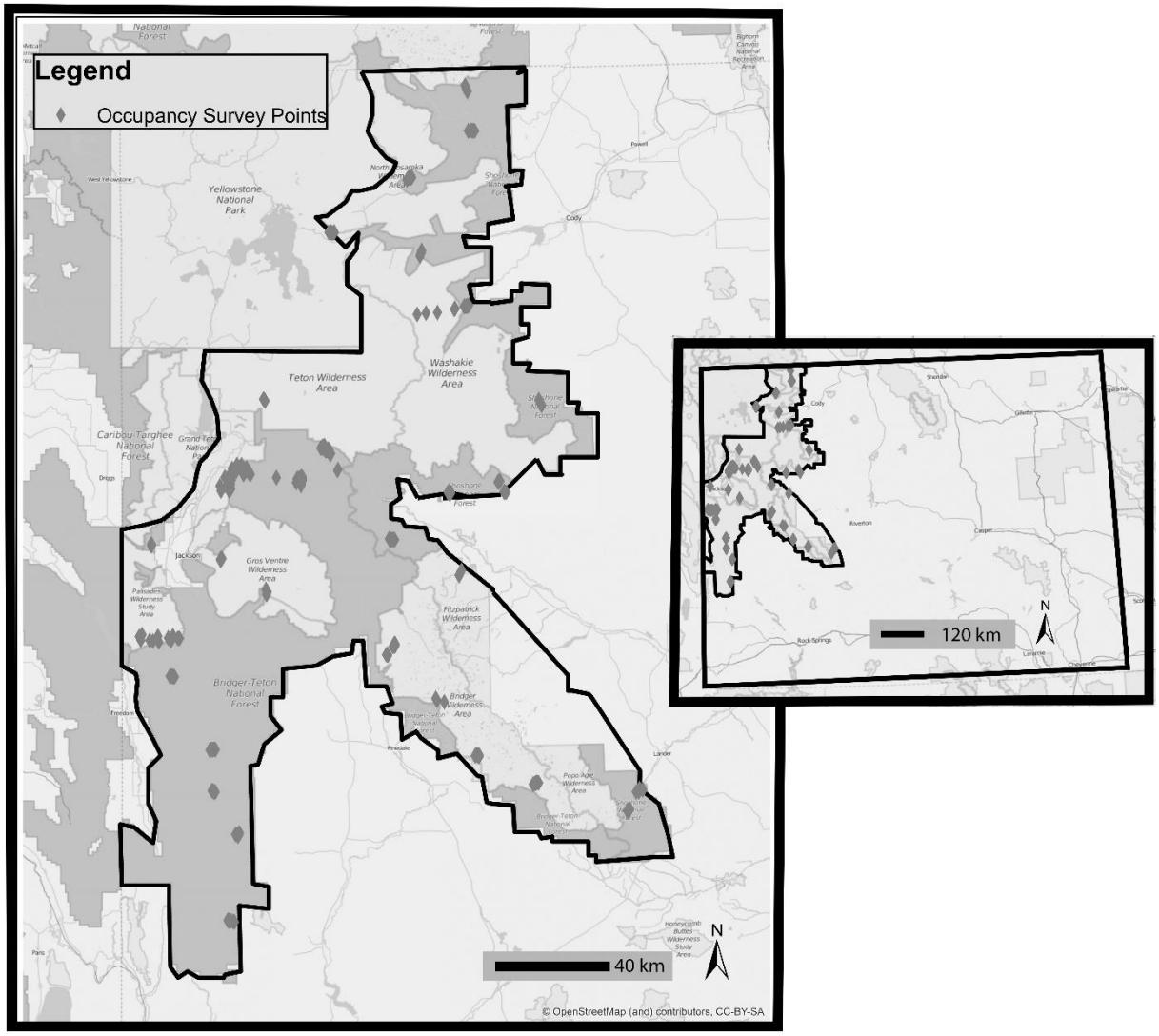


Figure. 4.1. Study area in the Greater Yellowstone Ecosystem. The inset map depicts the study area within the state of Wyoming. (OpenStreetMap basemap: http://www.openstreetmap.org/copyright [56].)

Stages of the annual cycle

We divided each year into five stages of the Clark's nutcracker annual cycle (Table 4.1). The divisions are biologically relevant, based on observations of variation in Clark's nutcracker behavior associated with life cycle stages and annual environmental changes.

2037 **Table 4.1. Dates of surveys during the five stages of the annual cycle.**

Stage of the annual cycle		**Associated dates of surveys**				
		2009	**2010**	**2011**	**2012**	**2013**
Breeding season	March 5, the first date in any year a Clark's nutcracker was seen building a nest, through June 15, the last date a nestling was observed on a nest.	NA	NA	Mar 15 – Jun 10	NA	May 19 – Jun 15
Early summer	June 16 through the day prior to when Clark's nutcrackers were observed eating immature whitebark pine seeds.	NA	NA	Jun 16 – Jun 30	Jun 22	Jun 16 – Jun 29
Late summer	Period during which Clark's nutcrackers were seed predators, eating immature whitebark pine seeds, but not yet caching mature seeds.	July 15 – Aug 11	July 15 – July 28	July 7 – Aug 3	July 12 – July 27	July 12 – Aug 9
Fall seed harvest stage	Period during which Clark's nutcrackers were potential seed dispersers, harvesting and caching mature whitebark pine seeds.	Aug 18 – Aug 30	NA	Aug 16 – Sept 15	Aug 13 – Sept 6	Aug 12 – Sept 28
Post-	Period during which we	Sept 9	NA	NA	Sept 10	Sept 29

harvest stage	observed no mature whitebark pine cones remaining on the trees.	– Sept 22			– Sept 27	– Oct 1

Clark's nutcracker occupancy point surveys

We established 238 random and 9 arbitrary occupancy point survey sites between 2009 and 2013. The points were located throughout Bridger-Teton and Shoshone National Forest, in or within seven km of whitebark pine habitat. Habitat at points included all six dominant conifer species. Schaming [14] documented whitebark pine, limber pine, Douglas-fir, lodgepole pine, Engelmann spruce, and subalpine fir at 52%, 22%, 33%, 38%, 48% and 64% of the 247 survey points, respectively. For details on point placement, see Schaming [14].

Each year, point count surveys were conducted at newly established points and a subset of points established in previous years. We carried out up to five surveys at each point each year. One survey consisted of three sequential ten-minute point counts, after an initial three-minute waiting period to minimize disturbance caused by our arrival. Three counts were necessary to evaluate detectability of Clark's nutcrackers as a function of habitats variables [19,20].

In addition to recording whether Clark's nutcrackers were detected through sight and/or calls, we recorded the distance to each observation. Flyovers were noted separately, but were included in the analyses [21]. Surveys were conducted when precipitation was absent or limited to light intermittent rain or snow.

Habitat surveys

Belt transects. To determine the annual number of cone-bearing whitebark pine trees per hectare, we conducted one set of belt transects at all points visited each year. We completed the

belt transects once whitebark pine cones were visible, typically mid to late July. One set of belt transects consisted of four separate belt transects, each 10 m wide and 50 m long, beginning from the survey point, and extending in each cardinal direction. The first 5 m of the western and eastern transects were discarded due to overlapping with the north and south transects. Therefore, a total of 1,900 m^2 was included in each survey. Within each belt transect, we counted the number of dead, live, cone-bearing, and live, non-cone-bearing whitebark pine trees >7 cm DBH (diameter at breast height; 1.4 m). All trees with green foliage were classified as ‘‘live’’, regardless of condition.

Cone counts. At each survey point, once cones were visible with binoculars, we randomly chose four cone-bearing whitebark pine trees for cone counts. Using a randomly selected azimuth bearing, we walked in the chosen direction from the point until we located the closest ovulate cone-bearing whitebark pine tree within 50 m. If four cone-bearing whitebark pine trees were not available within 50 m, we counted cones on as many as were available. Whitebark pine trees regularly grow in clusters; we considered each stem that split from a clump below 1.4 m to be a separate tree. Each year, we counted the number of new cones on the same four randomly chosen trees. We counted cones twice at each point in 2009, the first count between July 12 and July 31, and the second count between August 21 and August 30. Between 2010 and 2013, we counted cones at every visit when cones were visible. If, between years, a tree had died, could not be relocated, or did not bear cones, we randomly chose a replacement tree. As long as there were cones at the first visit, we did not replace a tree that did not have cones on subsequent visits within that year. We counted the number of new cones versus previous years’ old cones with handheld binoculars. Each cone was classified as whole, containing a “dished out” seed harvesting scar (a sign of nutcracker occurrence [22]), or stripped

(all scales removed, a sign of nutcracker occurrence [22]). We flagged each cone tree, and recorded their coordinates with a global positioning system unit (GPS; Garmin International, Olathe, Kansas, USA).

Point quarter method. We used a modified point quarter method to determine tree species, density, frequency, coverage (basal area), and importance value at survey points [23]. We conducted point quarters once per location during the five-year study period. At each survey point, we carried out a point quarter at the survey point, and at four additional points, 30 - 35 m to the northwest, northeast, southwest and southeast. At each of the five points, we divided the area into four quadrants, along north-south and east-west axes. In each quadrant, we documented the species of, and measured the circumference (±0.1 cm) of, and distance (m) to the closest live tree, and the circumference of and distance to the closest live and dead whitebark pine tree. We noted presence of mountain pine beetles and blister rust on all live whitebark and limber pine trees. If no trees and/or no live and/or dead whitebark pine trees were present within 200 m, the quadrant was labeled as empty for that category. Due to logistical complications, we were unable to complete the point quarter method at one of the 238 occupancy survey points. We noted elevation, slope, aspect, and general site conditions at each point.

Statistical analyses

Cones per hectare

For each survey conducted while whitebark pine cones were visible, we determined the associated number of whitebark pine cones per hectare. First, each year, we calculated the number of cone-bearing whitebark pines per hectare, and the average number of cones during each cone count. Then, multiplying the number of cone bearing trees per hectare by the average number of cones, we calculated an index of whitebark pine cones per hectare.

Local whitebark pine and Douglas-fir habitat

We used the point quarter data to determine the DBH, basal area per ha, and importance value of each tree species at each point (Table 4.2). We used importance value as the measure of local habitat because it incorporates relative frequency, relative density, and relative cover, instead of assuming one of the three variables is an adequate measure of a species' importance or dominance. Previous Clark's nutcracker surveys in whitebark pine habitats used basal area as a measure of local whitebark pine habitat [11,12]. To validate comparisons with previous studies, we computed the Spearman rank correlation, between basal area per hectare and importance value at the 238 random points as a measure of association. Managers regularly use whitebark pine basal area as a surrogate for cone crop when predicting probability of nutcracker visitation [11,17,18]. We therefore also used a Spearman rank correlation test to quantify the relationship between basal area and cone crop.

Table 4.2. Methods used to calculate habitat variables.

Variables	Calculations	Clarification
DBH (cm)	Circumference / π	NA
Basal area/ha (m^2)	$((DBH / 2)^2 * \pi) / 10{,}000$	NA
Relative frequency	(frequency of the species / total frequency of all species) * 100	Frequency = number of sample points at which the species occurs.
Relative density	(# individuals of the species / total # of	NA

	individuals of all species) * 100	
Relative cover	(cover of the species / total cover of all species) * 100	Cover = density for the species * average basal area for the species.
Importance value	relative frequency + relative density + relative dominance	NA

Landscape scale whitebark pine and Douglas-fir

We determined the area of whitebark pine and Douglas-fir habitat on the landscape with a land cover type map in ArcGIS. First, we constructed a geospatial layer of land cover types using map data from the whitebark pine stand-level condition assessment [17] and four national forest, national park and GAP analysis maps. For details on the construction of the geospatial layer, see Schaming [14].

In ArcGIS (10.1, ESRI), we created a 32.6 km radius buffer around each point, and calculated the area of whitebark pine habitat within each buffer. We used a buffer of 32.6 km because Clark's nutcrackers are known to travel up to 32.6 km from their summer home range to harvest seeds [8]. We evaluated if this was an appropriate measure of landscape scale to use in analyses [24]. First, we determined predictor values at multiple scales by systematically increasing the radius of the buffer around a subset of points (the 2009 – 2012 sample points; n = 103), by 1 km increments, up to 33 km. Then, we calculated the area of whitebark pine within

each buffer. To find the largest increment for which $r_s > 0.70$ for all predictors, we conducted Spearman rank correlations between the area of whitebark pine within 1 km and each other buffer, 2 km – 33 km [24]. All r_s were > 0.70, so we considered a 32.6 km buffer appropriate. We then determined the area of Douglas fir within 3.2 km of each point, the median diameter of a breeding season home range [16].

Naïve occurrence, comparisons with previous research

We used mixed models (glmer) in the "lme4" package [25] in R [version 3.1.2; ,26] to evaluate fall harvest naïve occurrence as a function of cone crop, with site ID and year as random variables. Naïve occurrence was the detection or not of Clark's nutcrackers from our occupancy surveys. We evaluated occurrence at radii of ≤100 m and an infinite distance separately (the set of models with the two radii is called the "pair of models"). We included data from all visits to each point during the fall harvest each year. We only examined fall harvest detections because this is the stage during which Clark's nutcrackers act as seed dispersers, rather than just seed predators [27]. First, we included all surveys in the pair of models. Second, we included all surveys with a whitebark pine importance value >0 (i.e. whitebark pine present at point) in the pair of models. Then, because the cone crop data was zero-inflated, we predicted that the sites without cones would have an outsize impact, and we analyzed a pair of models to evaluate fall harvest naïve occurrence as a function of presence or absence of whitebark pine cones. Finally, we fit a pair of models to evaluate fall harvest naïve occurrence as a function of cone crop, only including surveys at points where cones were present. We scaled the cone crop data for the final ≤100 m radius model to enable model convergence.

We compared our naïve occurrence results to the predictions of McKinney et al. [11] and Barringer et al. [12]. To be consistent with the other protocols, we included all the surveys at

which whitebark pine was present (whitebark pine importance value >0), cone crop density was >0, cones were counted on the same day as the occupancy survey, and survey date was between July 15 and September 15. First, we calculated the squared log of the cone crop density per hectare, the index of cone production used by McKinney et al. [11], from each of our cone counts. We converted infinite radius occurrence data to the proportion of hours with at least one detection. McKinney et al. [11] and Barringer et al. [12] predicted Clark's nutcracker occurrence as a function of cone production, using the linear regression model y = -0.449 + 0.019x, and the beta regression model y = (e^(-1.5165+0.03883*A2))/(1+e^(-1.5165+0.03883*A2)), respectively. For each cone count, we determined the predicted proportion of hours with at least one detection for the cone crop density index, using both functions. We used Spearman rank correlations to evaluate if there was a correlation between proportion of hours with at least one detection from our infinite radius fall harvest survey data and the predictions from McKinney et al.'s [11] and Barringer et al.'s [12] functions. Then, we used one-tailed Wilcoxon signed-rank tests to evaluate if the two previous models significantly underpredicted the probability of nutcracker occurrence at the survey points.

Occupancy models

We used occupancy models to evaluate whether whitebark pine cone crop, or whitebark pine or Douglas-fir at local or landscape scales influenced Clark's nutcracker occurrence during each stage of the annual cycle. MacKenzie et al. [19] used probabilistic arguments to construct a likelihood method for estimating probability of detection (p) based on repeated site visits and, by accounting for imperfect detection, the proportion of sites occupied (ψ). We followed this approach, and recorded the detection, or not, of nutcrackers during each 10 min point survey. Non-detection resulted from either a true absence, or Clark's nutcrackers being present but not

detected. Using detection non-detection data from the point surveys, we estimated site- and stage-specific detection (p), and occurrence probability (ψ) as a function of survey and site specific covariates.

For each stage, we included only covariates hypothesized to be biologically relevant for each particular stage based on Clark's nutcracker ecology (Table 4.3) [14,16]. Clark's nutcrackers only foraged on whitebark pine cones during the late summer and fall harvest. We predicted local presence of whitebark pine would only influence Clark's nutcracker occurrence during early summer when Clark's nutcracker presumably scouted for future seed sources, and during the late summer and fall harvest when the birds were harvesting the seeds. We predicted that the area of whitebark pine on the landscape would influence the birds' occurrence throughout the year, since even when the birds were not harvesting seeds, they would be consuming seeds previously harvested and cached within 32.6 km of the harvest trees, or scouting for future seed sources. We observed Clark's nutcrackers regularly harvesting Douglas-fir seeds in the late winter and breeding season, and harvesting and caching Douglas-fir seeds during the postharvest stage [Schaming personal observation, 16]. Douglas-fir habitat was also consistently selected for breeding season home range [16]. Therefore, we predicted local presence of Douglas-fir, and area of Douglas-fir on the landscape would impact Clark's nutcracker occurrence during the breeding season and postharvest stages. When modeling detectability, we included tree density for all stages because it seemed more difficult to both see and hear birds in sites with higher tree density (Schaming personal observation). We included whitebark pine importance value as a predictor for fall harvest detectability, because during that time, the birds seemed to call more loudly and frequently, and to move in larger, noisier groups when foraging on whitebark cones (Schaming personal observation). In Table 4.3, we provide details of the stage-specific

2200 covariates considered in the occupancy models.

2201 **Table 4.3. Predictor variables originally included in the single-season occupancy models.**

Predictor variables	**Breeding season**	**Early summer**	**Late summer**	**Fall harvest**	**Post-harvest**
Probability of occurrence					
WBP* cone crop density			x†	x†	
WBP importance value		x	x	x	
Area of WBP on landscape	x†	x†	x†	x†	x†
Douglas-fir importance value	x				
Area of Douglas-fir on landscape	x†				x†
WBP cone crop density **X**** WBP importance value			x	x	
WBP cone crop density **X** Area of WBP on landscape			x	x	
WBP importance value **X** Area of WBP on landscape		x	x	x	
Douglas-fir importance value **X** Area of WBP on landscape	x				
Area of WBP on landscape **X** Area of Douglas-fir on landscape	x				x
Detection					
Tree density	x	x	x	x	x
WBP importance value				x	

Tree density **X** WBP importance value				x	

*WBP is the abbreviation for whitebark pine.

** **X** signifies an interaction.

† Included in final analysis.

Because whitebark pine cone crop density and whitebark pine and Douglas-fir importance values were extremely zero-inflated, each was included both as a binary (present/absent) and continuous (>0) covariate. For example, by including the whitebark pine importance value covariate as both binary and continuous, we were able to ask if the probability of Clark's nutcrackers occupying a site depended on if there whitebark pine trees present at the site or not. Then, if occurrence was influenced by the presence of whitebark pines, did the probability of occurrence change in relation to the area of whitebark pine? Each covariate form only appeared if the other was in the model. All predictor variables were z-score standardized and, using Spearman rank correlations, we determined that covariates were not correlated in a way that would influence the resulting inference.

We modeled year- and stage-specific detection probability as a random effect with a single mean and standard deviation. We treated each year as independent because we had predicted *a priori* that regional abundance and behaviors of birds that influenced detection, but not occurrence, may have differed between both stages and years. Due to small sample sizes during some year-stage combinations, we modelled year and stage covariate effects as covariate-specific random effects, i.e., with a covariate-specific mean and standard deviation. In addition, when modeling detection, we included an additional observation level random effect to account

for lack of model fit. We only included occurrence data from the first visit (three ten-minute surveys) to each random point during each stage each year, and included 'site' as a random effect to account for repeated visits to the same site during the same stage over multiple years.

The models met the following key assumptions [20]. One, species can be never detected by error when actually absent. Two, the number of individuals available for detection must vary among counts, resulting in variation in detection probability. Three, detection events must be independent. Four, occurrence and detection probability are assumed to be similar across sites and time, except when the difference is modeled with covariates. The fifth assumption, that the population must be demographically closed to changes in occurrence during the sampling period (the three counts at each visit), was partially violated [20]. The size of the area surveyed was small compared to the size of a Clark's nutcracker home range, and the species may have been temporarily absent during a survey. This random temporary absence can be viewed as a random process, resulting in a slight violation of the demographic closure assumption being acceptable This assumption can be relaxed by an alternative interpretation of the model parameters such that "occupancy" was interpreted as "use" and detection as "in the site and detected" [20]. We therefore evaluated "occurrence" (use) rather than of "occupancy".

We adopted a Bayesian analysis of the occupancy model because of the flexibility it afforded in terms of incorporating all of the stage-year data, regardless of number of sites sampled, and to incorporate the random effects structure [28]. We fit a model for each survey radius, ≤100 m and an infinite distance. We fit the data with JAGS [29] through the "jagsUI" package [30] in R. We used vague priors for all hyperparameters, and posterior distributions were approximated using three 60,000 Markov chain Monte Carlo (MCMC) iterations with a burn-in of 20,000 iterations, and thinning rate of 1. Chains were visually diagnosed to confirm

convergence.

We used cross-product Bayesian model selection [31] to evaluate the importance of covariates and model structure. Bayesian model selection was not required for detection, because no covariates were included in the final detection model. Based on Barbieri and Berger's [32] threshold for the mean posterior inclusion probability we excluded all covariates that received an inclusion probability of $P(I_j = 1 \mid \boldsymbol{y}) \leq 0.5$. This criterion is useful, and recommended, for reducing the model space by removing variables with a small marginal inclusion probability [32,33]. For occurrence, at both radii considered, the final global candidate model set included four predictor variables. The model space for each stage was further refined based on the *a priori* predictions. The subset of candidate models used in the final analysis are shown in Table 4.3.

Using cross-product model selection, a posterior distribution of the binary indicator variable was generated, representing the number of iterations in which each model was selected. This posterior therefore represents the *model probability*, or the probability that model *m* was the best model from the candidate set *M*. The cross-product approach provides a posterior distribution of the identity of the model accepted in each iteration (i.e. of model support) which in turn identifies which covariate effects are in the model. Using this structure, summarizing the posterior distribution for any parameter conditional on whether it is contained within the supported model conveniently yields model averaged estimates. We also computed covariate importance by summarizing the posterior inclusion probability of each covariate across all models. In the final model set for both radii, each parameter was included in an equal number of models.

To assess model fit, we implemented a Bayesian version of the MacKenzie and Bailey [34] goodness-of-fit test. For both radius models, the 95% Bayesian Credible intervals (BCI) did

include 0, suggesting adequate fit (95% BCI = -1.37 – 0.46 and -0.59 – 1.65, respectively).

Predictability of whitebark pine cone crop

We evaluated if managers could reasonably use a relatively stable measure of whitebark pine habitat, such as basal area, importance value or area on the landscape, as a proxy for cone crop. First, we fit a negative binomial model to evaluate if cone crop in 2009 predicted cone crop at the site in 2011, using the "MASS" package [35] in R. We compared the largest set of paired points between two years at which >0 cones were observed, the 21 points we visited during the late summer in both 2009 and 2011. Then, for all points with a whitebark pine importance value >0, we evaluated if the whitebark pine importance value predicted the average number of cones per hectare, from the first count per year, over five years, using a zero-inflated negative binomial model using the "pscl" package [36] in R.

To determine if cone crop at the fall harvest stage varied with whitebark pine health, we fit a mixed model in the "lme4" package in R, with a Poisson distribution, and with site ID and year as random variables. To determine overall significance, we then used an ANOVA to compare a pair of models, one with and one without the health effect. Health was included as a categorical variable with four levels, low, moderate to high, high and very high mortality whitebark pine. Only points with cones present were included in the analysis. To examine the variation in cone crop as a function of whitebark pine health in an average year at an average point, we computed and compared the least-squares means in a linear model with the "lsmeans" package [37] in R.

Other

We used R to perform all analyses, unless otherwise stated. We checked for normality and homogeneity of variance, and met all key assumptions underlying application of general

linear and general linear mixed models. We applied $p \leq 0.05$ as the significance level, and report means ± standard error of the mean.

Data

All of the original data from which this article is based are deposited at Figshare https://figshare.com/articles/Data_for_paper_Clark_s_nutcracker_occurrence/3494312. Four sets of habitat maps were obtained from third parties and are available upon request. Data from the whitebark pine stand-level condition assessment are available from The Greater Yellowstone Whitebark Pine Subcommittee (contact the current committee chair listed on http://fedgycc.org/WhitebarkPineOverview.htm). The Bridger-Teton National Forest and Grand Teton National Park maps can be obtained from Nancy Bockino (Nancy_Bockino@nps.gov, Grand Teton National Park). The Shoshone National Forest maps can be obtained from Janice Wilson (janicewilson@fs.fed.us, U.S. Forest Service Rocky Mountain Region Regional Office, Geospatial Services). Wyoming GAP analysis vegetation maps are available online from the U.S. Geological Survey National Gap Analysis Program Land Cover Data Portal (http://gapanalysis.usgs.gov/gaplandcover/).

Results

Habitat

Habitat varied considerably between the 238 points (Table 4.4). The basal area per hectare and importance value of whitebark pine were highly positively correlated (rho = 0.9, $p < 0.001$). Between 2009 and 2013, we counted cones at each point an average of 2 years (± 0.07 SEM; range 1 - 5). The basal area per hectare was only moderately positively correlated with the average cone density per hectare (average of the first cone count per year, across all years; rho =

0.6, $p < 0.001$). Whitebark pine cones were present and visible as early as July 12 and as late as September 29.

Table 4.4. Habitat variables at 238 random points.

	Mean ± SEM	**Median**	**Range**	**# Sites where present versus absent**
Whitebark pine cone crop density (cones/ha) [all points; only points with cones]*	258 ± 28; 916 ± 48	0	0 – 8,132	82 versus 156 (>0 cones in ≥1 year versus 0 cones in all years)
Basal area/ha [all points; only points with whitebark pine]	1.3 ± 0.2; 2.6 ± 0.3	0.03; 1.0	0 – 18.5; 0.006 – 18.5	NA
Whitebark pine importance value	57 ± 5	16	0 - 305	122 versus 115 (importance value >0 versus 0; 1 NA)
Douglas-fir importance value	51 ± 5	0	0 - 300	81 versus 156 (importance value >0 versus 0; 1 NA)

Area of whitebark pine within 32.6 km (ha)	44,997 ± 1,294	44,068	2,916 – 87,259	NA
Area of Douglas-fir within 3.2 km (ha)	324 ± 24	228	0 – 1,754	NA

*Includes cone counts for the first survey per stage of the annual cycle each year, then first survey per stage when cones were present.

The sub-watershed was the minimum mapping unit for the landscape scale measure of whitebark pine, and therefore, the data could not reliably be used for stand-level mortality calculations [38]. Sub-watersheds have discrete geographic boundaries, which form natural breaks delineated by ridgelines [38]. However, whitebark pine at the local scale measured in the field, and landscape scale, determined via ArcGIS, were reasonably consistent. The mean distance to whitebark pine habitat for points with a local whitebark pine importance value >0 (i.e. whitebark pine present at the point) was 0.1 ± 0.02 km (n = 247; range = 0 – 1.5), while the mean distance for points with a local whitebark pine importance value of 0 (i.e. no whitebark pine present) was 2.0 ± 0.1 km (n = 201; range = 0 – 7.3).

Naïve occurrence, comparisons with previous research

Naïve occurrence at all points (three ten-minute counts combined) was 42% for ≤100 m radius and 64% for infinite radius (n = 869; Table 4.5). The probability of observing at least one Clark's

nutcracker during the fall harvest was positively, and significantly, associated with whitebark pine cone crop density for the ≤100 m radius data (n = 448; β= 0.002 ± 0.006, p = 0.008) and the infinite radius data (n = 448; β= 0.004 ± 0.002, p = 0.03). On the other hand, when only considering sites where whitebark pine was present, the likelihood of detecting a nutcracker increased significantly with cone crop density using the ≤100 m radius data (n = 249; β= 1.2 ± 0.4, p = 0.004), but not with the infinite radius data (n = 249; β= 0.9 ± 0.5, p = 0.1). In other words, cone density predicted the probability that a nutcracker was observed in sampling locations both in and near whitebark pine trees, although it is important to note that many sites did not have whitebark pines present. However, when comparing sites where whitebark pine trees were present, only the ability to observe a nutcracker ≤100 m could be adequately predicted.

Table 4.5. Naïve occurrence during each stage of the annual cycle.

Stage	**Points occupied (%)**		**Total number of points**
	≤100 m radius	**Infinite radius**	
Breeding season	14	20	128
Early summer	14	27	63
Late summer	51	78	333
Fall harvest	45	71	276
Postharvest	67	80	69

Observing a nutcracker during the fall harvest was positively, and significantly, associated with the presence of whitebark pine cones for both radii (n = 448; β= 1.3 ± 0.4, p = 0.0003, and β= 1.4 ± 0.5, p = 0.005, for ≤100 and infinite respectively). However, when only

including surveys with >0 cones, the cone crop per hectare did not significantly predict occurrence at either radii (≤100 m: n = 118; β= 0.6 ± 0.5, p = 0.3, or infinite: β= 0.002 ± 0.002, p = 0.3). In other words, when there were whitebark pine trees at a location, the presence of cones, but not the number of cones, was a better predictor of the probability of whether or not Clark's nutcrackers were observed.

The proportion of hours with at least one detection from our infinite radius fall harvest data was only weakly positively correlated with that predicted by McKinney et al. [11] and Barringer et al. [12] (n = 110; rho=0.3, p = 0.008, and rho = 0.3, p = 0.006). Both previous models significantly underpredicted the proportion of observation hours resulting in Clark's nutcracker observations in our study, based on an equivalent cone production index (n = 110; W = 714.5, $p < 0.0001$, and W = 1096.5, $p < 0.0001$, respectively; Fig. 4.2).

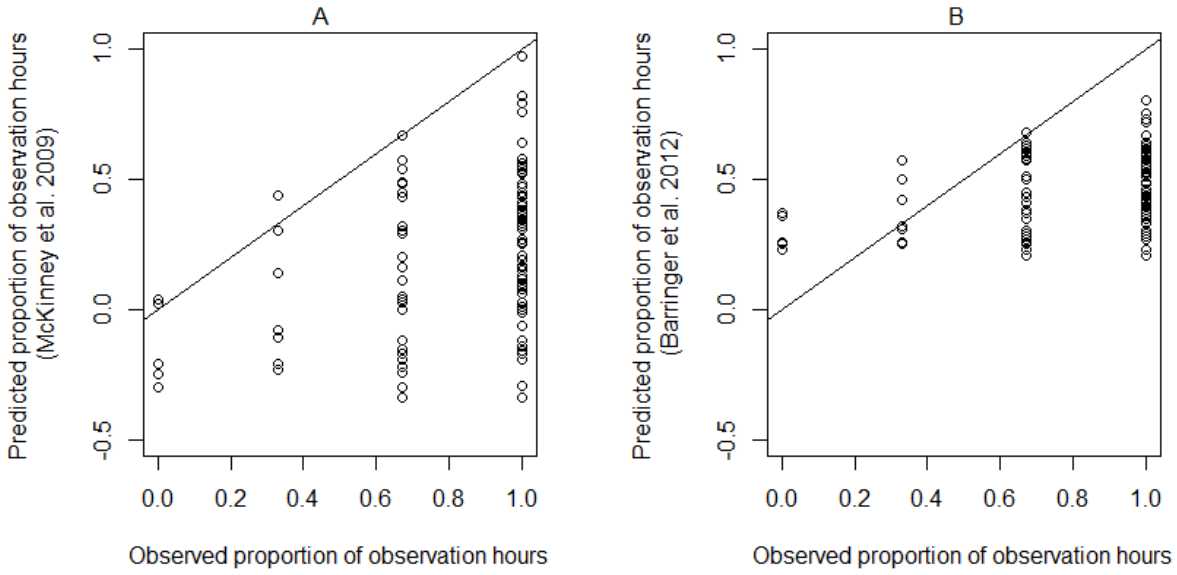


Figure. 4.2. Observed proportion of observation hours with Clark's nutcracker occurrence versus proportion of hours predicted from cone production index using (A) McKinney et al.'s [11] **and (B) Barringer et al.'s** [12] **models.** The diagonal line represents a perfect

prediction from the model (1:1). Both previous studies underpredicted the probability of naïve Clark's nutcracker occurrence.

Occupancy models

Occupancy models included data from 2,526 surveys (Table 4.6). Detection varied across stages and years with a general trend of increasing detectability through the year. Detection was relatively low during the breeding season, moderate during the early and late summer, and relatively during the fall harvest and postharvest stages (Table 4.7 and Fig. 4.3). Within-year variation was highest in late summer and certainty in detection probabilities reflected variation in sample sizes (Table 4.7 and Fig. 4.3).

Table 4.6. Number of surveys per stage of the annual cycle included in occupancy models.

Stage of the annual cycle	Sample size					
	2009	**2010**	**2011**	**2012**	**2013**	**Total All Years**
Breeding season	0	0	123	0	261	**384**
Early summer	0	0	51	6	132	**189**
Late summer	144	3	189	6	411	**753**
Fall harvest	144	0	165	72	612	**993**
Postharvest	144	0	0	45	18	**207**

Table 4.7. Posterior mean year-stage detection probabilities and 95% Bayesian Credible Intervals. Dashes indicate stage-year combinations without data.

Year	**2009**	**2010**	**2011**	**2012**	**2013**
Fall whitebark pine cone crop [55]	**very high**	**low**	**medium**	**high**	**low**
≤100 m radius					
Breeding season	-	-	0.10 (0.01,0.52)	-	0.27 (0.06,0.58)
Early summer	-	-	0.41 (0.07,0.83)	0.36 (0.05,0.82)	0.19 (0.02,0.6)
Late summer	0.39 (0.21,0.62)	0.30 (0.02,0.83)	0.32 (0.16,0.53)	0.74 (0.28,0.98)	0.29 (0.13,0.5)
Fall harvest	0.60 (0.46,0.74)	-	0.67 (0.48,0.81)	0.66 (0.43,0.84)	0.23 (0.11,0.4)
Post-harvest	0.64 (0.43,0.81)	-	-	0.68 (0.4,0.88)	-
Infinite radius					
Breeding season	-	-	0.03 (0,0.3)	-	0.22 (0.07,0.53)
Early summer	-	-	0.53 (0.15,0.87)	0.45 (0.04,0.93)	0.49 (0.12,0.85)
Late summer	0.69 (0.51,0.84)	0.33 (0.01,0.95)	0.61 (0.41,0.78)	0.92 (0.44,1)	0.57 (0.43,0.71)

Fall harvest	0.88 (0.79,0.94)	-	0.87 (0.75,0.94)	0.75 (0.53,0.9)	0.64 (0.5,0.74)
Post-harvest	0.89 (0.78,0.96)	-	-	0.95 (0.82,0.99)	-

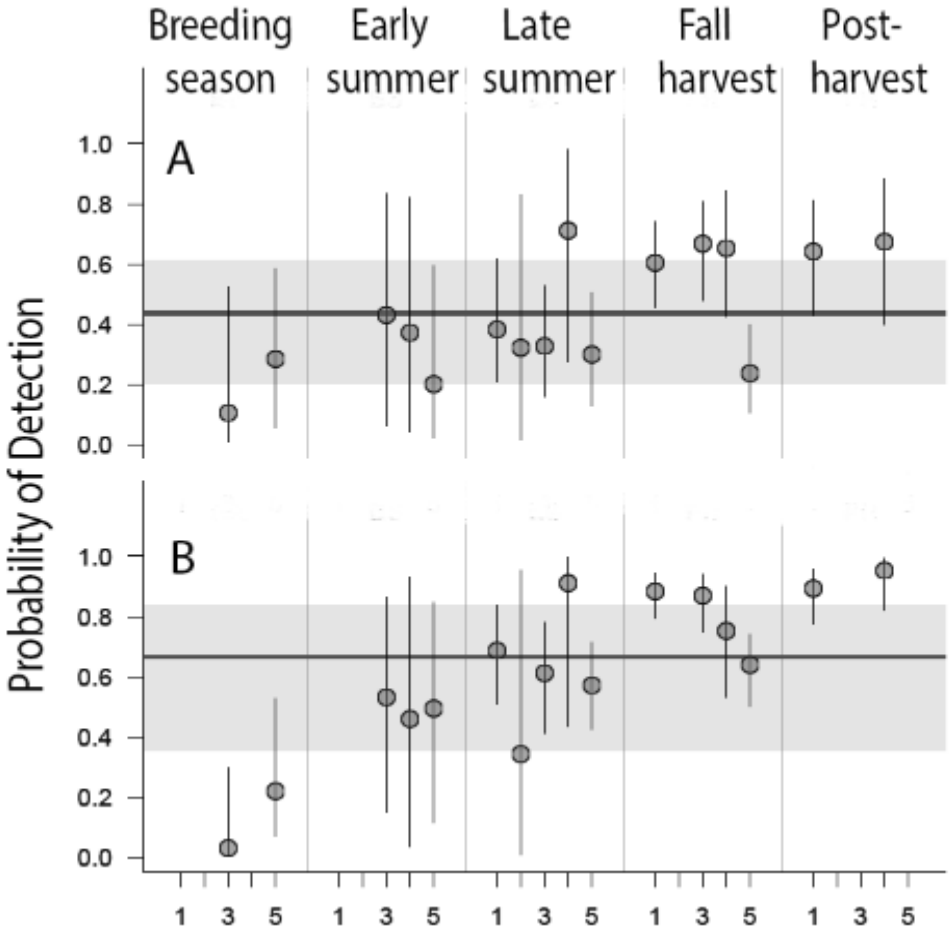


Figure. 4.3. Posterior mean year-stage detection probabilities (red circles) and 95% Bayesian Credible Intervals (BCI; vertical black lines) of the (A) ≤100 m radius, and (B) infinite radius data. Year-stage parameters are random effects from a hyper-distribution represented by the blue horizontal line (the posterior mean of the mean), the blue shaded area represents the 95% BCI of the estimate mean. Years 1 – 5 represent 2009 – 2013.

As expected, our results suggest that Clark's nutcracker occurrence varies between stages of the annual cycle (Tables 4.8 and 4.9). Whitebark pine cone crop density, and area of whitebark pine and Douglas-fir on the landscape affected occurrence regardless of radius data used. Occurrence was not, however, influenced by either whitebark pine or Douglas-fir importance value. The survey radius slightly altered the extent to which variables impacted occurrence.

Table 4.8. Stage-specific posterior occupancy model probabilities. Dashes indicate stages in which effects were constrained to be 0 (i.e. were not considered).

	M1	**M2**	**M3**	**M4**	**M5**	**M6**
Covariates						
Intercept	X	X	X	X	X	X
Whitebark pine cone crop density (binary)		X			X	
Whitebark pine cone crop density (continuous)		X			X	
Area of whitebark pine on the landscape			X		X	X
Area of Douglas-fir on the landscape				X		X
Stage of the annual cycle						
≤100 m radius						
Breeding season	0.12	-	0.03	0.74	-	0.18
Early summer	0.70	-	0.30	-	-	-

Late summer	0.09	0.50	0.27	-	0.13	-
Fall harvest	0.00	0.29	0.08	-	0.63	-
Postharvest	0.50	-	0.15	0.24	-	0.11
Infinite radius						
Breeding season	0.02	-	0.00	0.69	-	0.29
Early summer	0.81	-	0.19	-	-	-
Late summer	0.23	0.34	0.30	-	0.14	-
Fall harvest	0.03	0.50	0.11	-	0.36	-
Postharvest	0.28	-	0.10	0.34	-	0.29

Table 4.9. Model averaged, or conditional, parameter estimates (± 95% Confidence Internals), and conditional posterior support for each parameter in the occupancy model. Posterior distribution of stage-specific parameter estimates, and conditional posterior support which shows how important is each covariate in predicting occurrence as compared to other parameters in the model set (in square brackets). Dashes indicate stages in which effects were constrained to be 0 (i.e. were not considered). Bolded results indicate that the CI's exclude 0 (i.e. there is an effect).

	Intercept	Whitebark pine cone crop density (binary)*	Whitebark pine cone crop density (continuous)	Area of whitebark pine on the landscape	Area of Douglas-fir on the landscape
≤100 m radius					

Breeding season	-0.86 (-1.93,1.42) [1.00]	-	-	0.39 (-0.58,2.23) [0.21]	**-1.39 (-3.09,-0.32) [0.92]**
Early summer	-1.03 (-2.46,1.26) [1.00]	-	-	-0.83 (-2.63,0.37) [0.30]	-
Late summer	2.72 (0.62,6.09) [1.00]	**-2.51 (-5.46,-0.32) [0.63]**	-0.37 (-2.07,1.52) [0.63]	1.25 (-0.05,3.72) [0.40]	-
Fall harvest	4.23 (2.37,6.84) [1.00]	**-3.61 (-6.28,-1.37) [0.92]**	0.57 (-1.82,2.4) [0.92]	**0.83 (0.15,2.53) [0.71]**	-
Postharvest	2.09 (0.69,5.79) [1.00]	-	-	0.9 (-1.70,4.63) [0.26]	0.78 (-3.41,4.18) [0.35]
Infinite radius					
Breeding season	0.27 (-1.14,2.79) [1.00]	-	-	0.87 (-0.24,2.54) [0.29]	**-2.06 (-4.77,-0.63) [0.98]**
Early summer	-0.5 (-1.38,0.7) [1.00]	-	-	-0.46 (-1.49,0.37) [0.19]	-
Late summer	3.75	-2.36	-0.27	1.25	-

	(1.44,7.14) [1.00]	(-5.2,0.99) [0.48]	(-2.45,1.86) [0.48]	(-2.33,3.72) [0.44]	
Fall harvest	5.22 (3.07,8.06) [1.00]	**-3.44** **(-6.26,-1.06)** **[0.86]**	-0.08 (-2.69,1.94) [0.86]	**0.83** **(0.01,2.25)** **[0.47]**	-
Postharvest	2.87 (1.36,5.31) [1.00]	-	-	1.11 (-0.69,3.32) [0.39]	2.36 (-0.89,6.23) [0.63]

Breeding season

During the breeding season, occurrence at both ≤100 m and infinite radii was best explained by area of Douglas-fir (-1.39 (CI = -3.09,-0.32) and -2.06 (CI = -4.77,-0.63), respectively) and whitebark pine (0.39 (CI = -0.58,2.23), and 0.87 (CI = -0.24,2.54), respectively) on the landscape, but the area of Douglas-fir was 3.4 - 4.4 times more important (Table 4.9). The ≤100 m and infinite radius models which included only area of Douglas-fir had 4.1 and 2.4 times more support than the models with both area of Douglas-fir and whitebark pine (Table 4.8). Probability of occurrence is predicted to decrease with a higher area of Douglas-fir on the landscape, and to increase slightly with an increase in area of whitebark pine (Fig. 4.4).

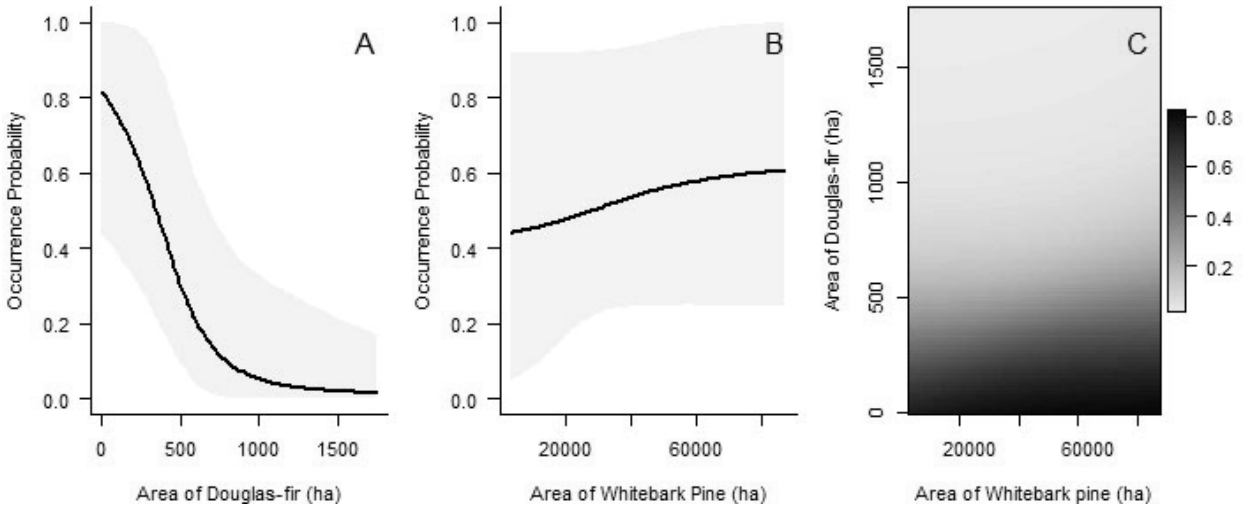


Figure. 4.4. Predicted probability of Clark's nutcracker occurrence during the breeding season as a function of area of Douglas-fir and whitebark pine on the landscape. The graphs depict predictions based on data from infinite radius surveys. Values represent area of whitebark pine habitat within 32.6 km and Douglas-fir habitat within 3.2 km. On each graph, all variables in the models that are not shown on the graphs, are held at the mean. Gray shaded areas denote 95% Bayesian Credible Intervals.

Early summer

For both the ≤100 m and infinite radii data, the intercept-only model, i.e., with no covariates, received most support (70% and 81%, respectively; Table 4.9). Although the area of whitebark pine on the landscape had the strongest influence on occurrence, the effect was weak (-0.83 (CI = -2.63,0.37) and -0.46 (CI = -1.49,0.37)), and the intercept-only model received 2.3 and 4.3 times more support for the ≤100 m and infinite radius data models respectively (Tables 4.8 and 4.9).

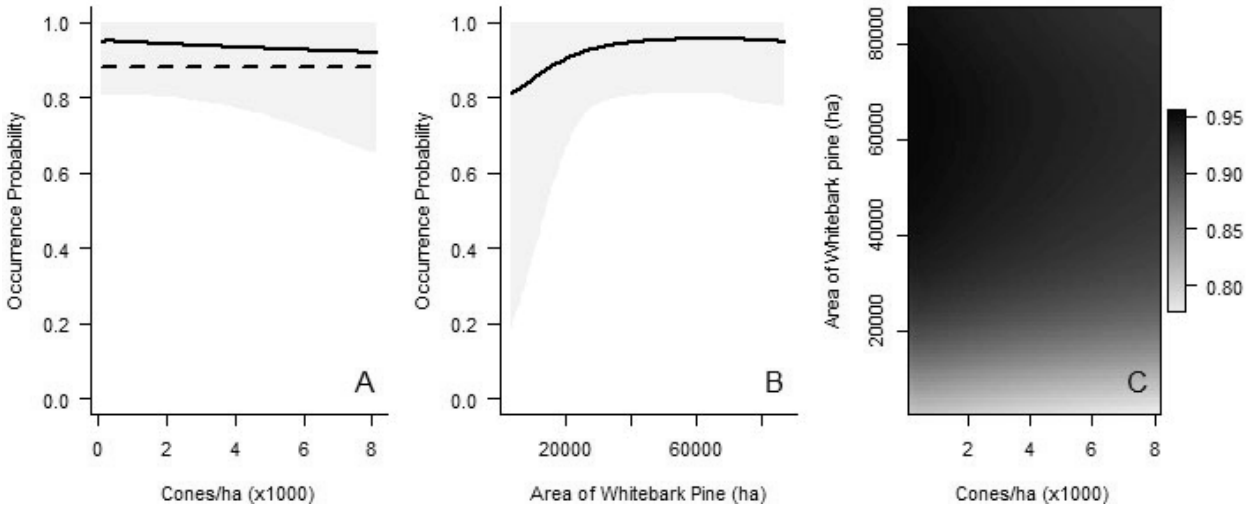
Late summer

During the late summer, when Clark's nutcrackers were harvesting immature cones,

presence or absence of cones (-2.51 (CI = -5.46,-0.32) and -2.36 (CI = -5.2,0.99) at ≤100 m and infinite radius, respectively) and the area of whitebark pine on the landscape (1.25 (CI = -0.05, 3.72) and 1.25 (-2.33,3.72), respectively) had a relatively strong influence on Clark's nutcracker occurrence (Tables 4.8 and 4.9). Based on the parameter estimates for the ≤100 m and infinite radius models, the presence or absence of cones at a site was 7 – 9 times more important than the number of whitebark pine cones (Table 4.9). At ≤100 m there was a 27 – 99.6% increase in the odds of a site being occupied if cones were present, regardless of the number per ha. However, at an infinite radius, the results were equivocal as the confidence intervals bounded zero.

Cone crop was only 1.1 – 1.6 times more important than area of whitebark pine (Table 4.9). At both radii, the model which included only cone crop density had approximately 1.9 and 1.1 times more support than the model which just included area of whitebark pine, and 3.8 and 2.4 times more support than the model which included cone crop and area of whitebark pine (Table 4.8). In other words, this variation in model support suggests that there are two different mechanisms, cone crop density and area of whitebark pine on the landscape which similarly increase the probability of Clark's nutcracker occurrence. A model which includes both includes redundancy, and is penalized for a higher number of variables. Hence including both variables is perhaps unnecessary. At ≤100 m radius, the top model had 5.6 times more support than the intercept only model, whereas at the infinite radius, it only had 1.5 times more support (Table 4.8).

At all cone crop levels, when a mean area of whitebark pine is present on the landscape, the probability of occurrence is predicted to be relatively high (Fig. 4.5). However, variability in probability of occurrence increases as the number of cones per hectare increases. A high probability of occurrence, ≥ approximately 75%, is predicted when the landscape is composed of a minimum of 8% cone-bearing whitebark pine habitat (~25,000 ha) within a 32.6 km radius.



2452

2453 **Figure. 4.5. Predicted probability of Clark's nutcracker occurrence during the late summer**
2454 **as a function of the cone crop and area of whitebark pine on the landscape.** The graphs
2455 depict predictions based on data from infinite radius surveys. Values represent area of whitebark
2456 pine habitat within 32.6 km. On each graph, all variables in the models that are not shown on the
2457 graphs, are held at the mean. Gray shaded areas denote 95% Bayesian Credible Intervals. In A,
2458 the reference horizontal line shows the intercept when no cones are present.

2459

2460 **Fall harvest**

2461 During the fall harvest, presence or absence of cones (-3.61 (CI = -6.28,-1.37) and -3.44
2462 (CI = -6.26,-1.06) at ≤100 m and infinite radius, respectively) and area of whitebark pine on the
2463 landscape (0.83 (CI = 0.15,2.53) and 0.83 (CI = 0.01,2.25)) both had a relatively strong influence
2464 on Clark's nutcracker occurrence. Whether or not cones were present at a site was 6 – 43 times
2465 more important than the number of whitebark pine cones (Table 4.9). At ≤100 m and an infinite
2466 radius, there was a 75 – 99.8% and 65 - 99.8% increase in the odds of a site being occupied if
2467 cones were present, respectively.

2468 Cone crop was only 1.3 – 1.8 times more important than the area of whitebark pine,

respectively (Table 4.9). At ≤100 m radius, the model which included cone crop density and area of whitebark pine had 2.2 times more support than the model which only included cone crop, and 7.9 times more support than the model which only included area of whitebark pine (Table 4.8). On the other hand, at an infinite radius, the model which included cone crop had 1.4 times more support than the model with both cone crop and area of whitebark pine and 4.5 times better than the model with only area of whitebark pine.

As cone crop increases, when a mean area of whitebark pine is present on the landscape, the probability of occurrence is predicted to be high and change very little (Fig. 4.6). However, when the minimum area of whitebark pine is on the landscape, variability of occurrence is high. Accounting for variability, a high probability of occurrence, ≥ approximately 75%, is predicted when the landscape is composed of a minimum of 4% cone-bearing whitebark pine habitat (~12,000 ha) within a 32.6 km radius. At a high level of cone crop, variability in the probability of occurrence is higher regardless of the area of whitebark pine.

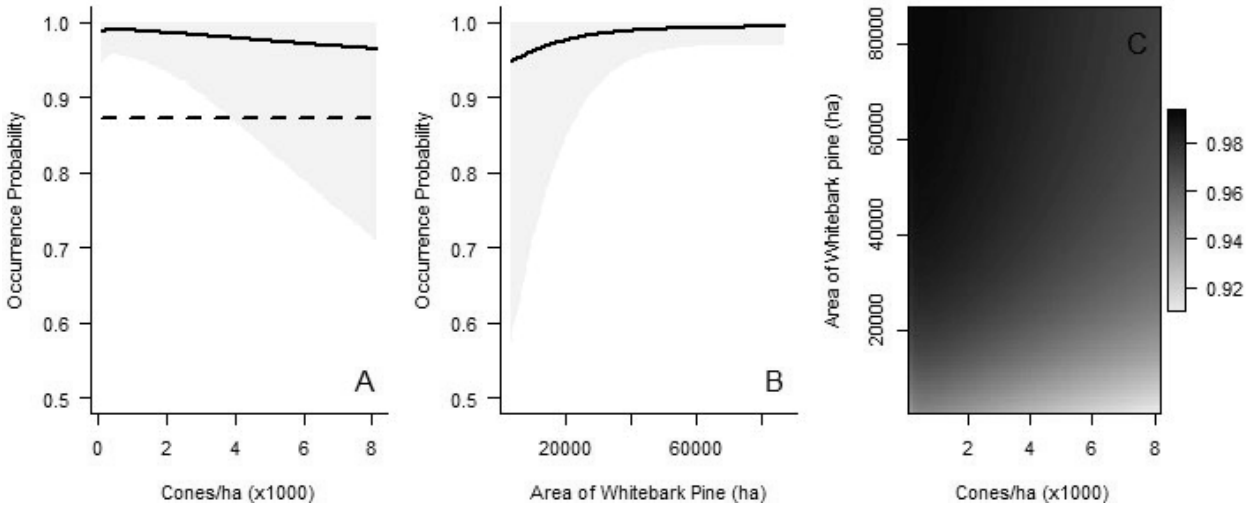


Figure. 4.6. Predicted probability of Clark's nutcracker occurrence during the fall harvest as a function of the cone crop and area of whitebark pine on the landscape. The graphs depict predictions based on data from infinite radius surveys. Values represent area of whitebark

pine habitat within 32.6 km. On each graph, all variables in the models that are not shown on the graphs, are held at the mean. Gray shaded areas denote 95% Bayesian Credible Intervals. In A, the reference horizontal line shows the intercept when no cones are present.

Postharvest

After whitebark pine cones were no longer available, both the area of Douglas-fir (0.78 (CI = -3.41,4.18) and 2.36 (CI = -0.89,6.23) at ≤100 m and infinite radius, respectively) and whitebark pine on the landscape (0.9 (CI = -1.70,4.63) and 1.11 (CI = -0.69,3.32)) had a relatively strong influence on Clark's nutcracker occurrence (Table 4.9). Area of Douglas-fir was 1.3 – 1.8 times more important than area of whitebark pine (Table 4.9). At ≤100 m radius, the intercept only model had approximately two times more support than the model containing area of Douglas-fir, 3.3 times more support than the model containing area of whitebark pine, and 4.5 times more support than the model with both areas (Table 4.8). However, at an infinite radius, the intercept only model, the model with area of Douglas-fir and the model with area of both whitebark pine and Douglas-fir had had approximately equal support.

During the postharvest stage, Clark's nutcracker occurrence was predicted to increase, then plateau, with an increase in the area of Douglas-fir on the landscape (Fig. 4.7). Variability was high when there was a relatively small area of whitebark pine. The probability of occurrence also increased with area of whitebark pine, and had the lowest variability at mean area of Douglas-fir. Overall, the highest variability in probability of occurrence is predicted when there is both low Douglas-fir and low whitebark pine. In fact, 0 probability of occurrence is only predicted in this situation.

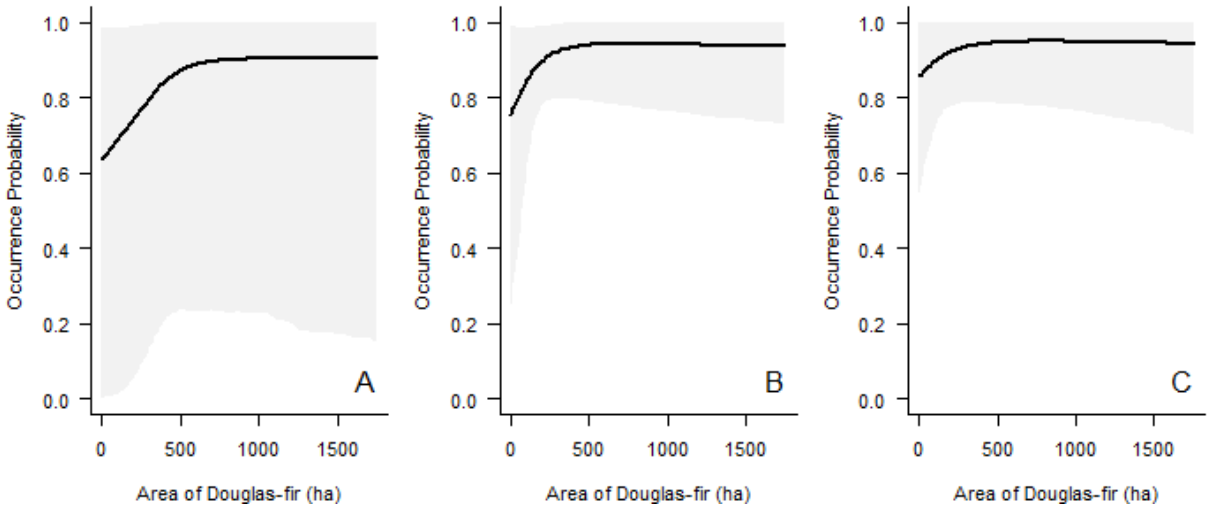


Figure 4.7. Predicted probability of Clark's nutcracker occurrence during the postharvest as a function of the area of Douglas-fir and whitebark pine on the landscape. The graphs depict predictions based on data from infinite radius surveys. Values represent area of Douglas-fir habitat within 3.2 km. Area of whitebark pine is held at the (A) minimum, (B) mean, and (C) maximum, and all other variables are held at the mean. Gray shaded areas denote 95% Bayesian Credible Intervals.

Predictability of whitebark pine cone crop

During the late summer, the number of cones at a point in 2009 did not predict the number of cones at the same point in 2011 ($n = 21$; $\beta = 0.00005 \pm 0.0002$, $p = 0.8$). On the other hand, at sites with whitebark pine (importance value >0), the whitebark pine importance value significantly predicted the average number of whitebark pine cones ($n = 122$, $\beta = 0.009 \pm 0.003$, $p = 0.0004$). The three outliers did not alter significance.

Fall surveys were conducted at points with four health levels: low mortality (n = 1), moderate to high mortality (n = 54), high mortality (n = 49) and very high mortality [16,n = 5; ,17]. The health of the whitebark pine habitat at the point significantly predicted the cone crop density (X^2

= 25.9, DF = 3, $p < 0.001$; Fig. 4.8). Low mortality stands had a higher cone crop density as compared to moderate to high and high mortality stands. However, very high mortality stands had an even higher average density, but variability was also high. The high variability surrounding the low and high mortality is likely due to low sample sizes at those levels.

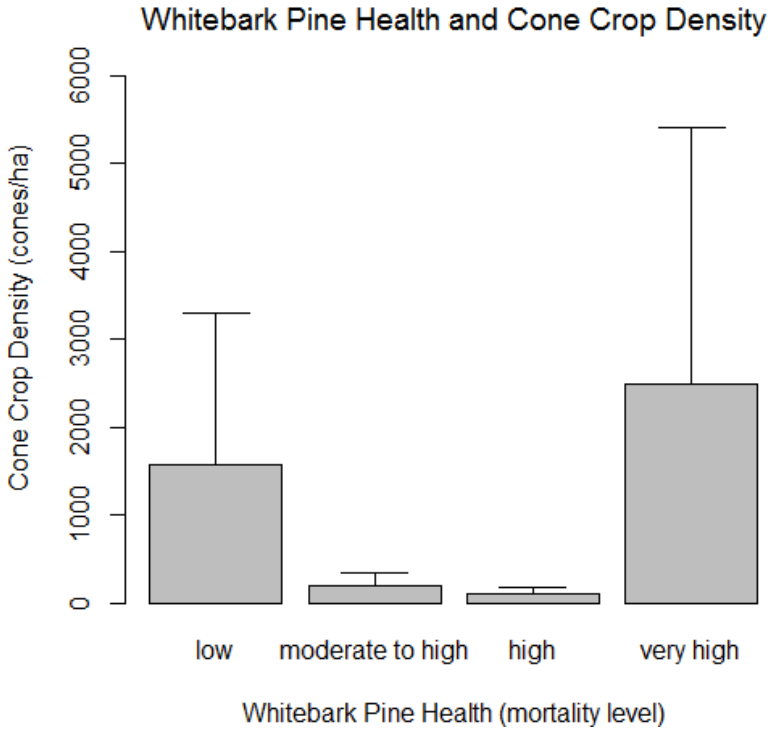


Figure. 4.8. Stand level whitebark pine health significantly impacted cone crop density.

Discussion

Our results suggest that, under current conditions in the southern Greater Yellowstone Ecosystem, Clark's nutcracker occurrence is associated with both the presence of cone-bearing whitebark pine trees and the proportion of habitat on the landscape composed of whitebark pine. Clark's nutcracker occurrence is far more strongly influenced by presence of whitebark pine cones rather than number of cones per hectare. In contrast, previous research has indicated that occurrence was associated with whitebark pine cone crop density and local basal area of

whitebark pines [11,12]. As a consequence, whitebark pine management efforts have focused on reaching a cone crop density of at least ~1,000 cones and a basal area of 5 m^2 per ha, the densities predicted to yield a high probability of Clark's nutcrackers at a site [11,17]. Instead, to encourage a high, >75%, probability of Clark's nutcracker occurrence, we suggest that management will be better served by ensuring the landscape is composed of a minimum of 8% cone-bearing whitebark pine habitat (~25,000 ha) within a 32.6 km radius, rather than attempting to achieve a specific cone and basal area density within a stand.

Alternatively, managers should consider focusing on increasing whitebark pine cone densities to saturate the Clark's nutcracker habitat. During the late summer, Clark's nutcrackers forage on immature whitebark pine seeds, acting as seed predators rather than seed dispersers [27]. At higher cone densities, there is higher variability in Clark's nutcracker occurrence in stands, suggesting Clark's nutcrackers are less likely to occupy all stands at once. As a result, a higher proportion of seeds would likely survive until maturity. During the fall harvest, Clark's nutcrackers continue harvesting and caching whitebark pine seeds as long as they are available, and during large cone crops, individuals have been estimated to cache 3 – 5 times more seeds than they need for their energetic requirements [39,40]. A lower cone crop leads to a shorter harvest, which likely translates into a lower number of seeds dispersed and a higher proportion of seeds retrieved per bird. Accordingly, at the current Clark's nutcracker population level, at higher cone densities in some stands, the higher variability in Clark's nutcracker occurrence should result in a longer harvest. Higher numbers of cached seeds and fewer retrieved caches would increase the potential for whitebark pine regeneration.

In addition, we suggest that management should focus on conserving a mosaic of whitebark pine and Douglas-fir on the landscape. During the postharvest stage, higher Clark's

nutcracker occurrence was associated with a moderate to high area of whitebark pine and a moderate area of Douglas-fir. In fact, low Clark's nutcracker occurrence was only likely at sites with a low area of both whitebark pine and Douglas-fir habitat. These results suggest that Clark's nutcrackers were not moving out of the whitebark pine habitats once the cone crop was depleted, and Douglas-fir habitat, which provided an alternate seed source, was generally only used when in a habitat mosaic with whitebark pine.

On the other hand, during the breeding season, Clark's nutcracker occurrence decreased with a higher area of Douglas-fir, regardless of the whitebark pine area. This was surprising because radio-tagged Clark's nutcrackers in the study area highly selected Douglas-fir habitat for their breeding season home ranges in two environmentally and demographically different years, 2011, when population wide-nonbreeding occurred following a low whitebark pine cone crop, and 2012, when breeding occurred following a medium cone crop [16]. However, although radio-tagged Clark's nutcrackers highly selected Douglas-fir habitat from the available habitat on the landscape, it only made up an average of 22 ± 3% of the total habitat within each bird's home range [n = 55; ,41]. In addition, when selecting habitats within the home ranges, the birds used Douglas-fir in proportion to availability [16]. Therefore, Douglas-fir habitat was only used by radio-tagged birds, on average, about a quarter of the time. The occurrence patterns reveal which resources were important drivers of the Clark's nutcrackers distribution and population dynamics, whereas habitat selection was the process by which individual birds select habitats relative to their availability [20,42]. The contradictory habitat use and selection results suggest that a habitat mosaic which contains Douglas-fir at low area is optimal. These results emphasize the importance of considering both the habitats used by Clark's nutcracker populations and the habitats individuals select when developing whitebark pine restoration strategies.

We suggest Clark's nutcracker habitat use should be separately evaluated in each ecosystem of conservation interest, or at a minimum in a greater number of ecosystems, before using cone crop density thresholds as a management criterion. Current whitebark pine restoration strategies incorporate goals of reaching whitebark pine cone crop and basal area thresholds, above which Clark's nutcrackers are predicted to have a high probability of occurrence [11,12,17]. However, there were discrepancies between our results and those from the two previous Clark's nutcracker occurrence models used to set these whitebark pine management goals [11,12,17]. We used the previous models to predict Clark's nutcracker presence at each of our points based on our observed cone crop density. Both models underpredicted the proportion of hours resulting in Clark's nutcracker observations in our study. In addition, in both our study and the previous research, higher Clark's nutcracker observations during the fall harvest were associated with higher whitebark pine cone crop density. However, in our study, once we accounted for detectability and included both presence/absence of cones and area of whitebark pine, in addition to cone crop density, occurrence was only weakly associated with cone crop density.

Our results emphasize the importance of accounting for detectability for a species with relatively low detection rates, particularly in fragile ecosystem. Failing to consider detectability would therefore have underestimated true occupancy rates [19]. By extrapolation, we suggest that the data used to generate the previous models underestimated true occupancy rates. Clark's nutcracker detectability varied between years and stages of the annual cycle, although surprisingly, it was not influenced by either tree density or dominance of local whitebark pines at a site. Due to the small sample size of only two to five years for each stage, we were unable to examine which annual variables influenced detection rates. Cone crop may have had an indirect

effect on Clark's nutcracker occurrence as Clark's nutcrackers are known to move out of an ecosystem in years with widespread low to moderate cone crops [43,44], and a lower area of birds may have decreased detectability. Also, population-wide nonbreeding occurs in the population [14]. Breeding birds were more secretive and quiet, and less likely to travel in flocks (Schaming personal observation). Therefore, in years when birds did not breed, detectability may have been higher. The variation in detectability between stages was likely a result of consistent changes in Clark's nutcracker foraging and social behavior throughout the year [45], however, using the random effects structure may have captured this between- and within-year variability.

In addition to accounting for detectability, our results may have differed from those of the previous models because we included cone crop density as both a binary and continuous variable, and included landscape scale habitat variables. When evaluating the impact of habitat on Clark's nutcracker occurrence, we teased apart the effect of simple presence versus the area of whitebark pine cones. We included both presence/absence of cones and cone crop density in our models because, like much ecological data, our cone crop densities were zero-inflated, and therefore sites without cones were likely to have an outsize impact. By doing this, we were able to conclude how much more important simple presence of cones was on Clark's nutcracker occurrence. Also, by using model selection to compare models which included one or more habitat variables, we determined that models which included both cone crop density and area of whitebark pine on the landscape during the fall harvest were better supported than models with only cone crop density. This suggests that area of whitebark pine on the landscape should be taken into account when setting management goals.

Due to the contradictions between our results and those of previous research, we suggest that management should reconsider basing their whitebark pine restoration strategies on the

earlier models. Alternatively, the earlier models may be accurate at predicting probability of Clark's nutcracker occurrence in more heavily degraded ecosystems which are experiencing higher levels of whitebark pine mortality, but this should be tested. Nevertheless, because current guidelines are not reasonable in the Greater Yellowstone Ecosystem, we suggest that current blanket guidelines should not be used over the entire Clark's nutcracker- whitebark pine range.

Stability of the Clark's nutcracker-whitebark pine mutualism

Currently, the Clark's nutcracker-whitebark pine mutualism appears to be functional in the Greater Yellowstone Ecosystem. As long as the birds are present locally, our results suggest they will continue to use cone-bearing whitebark pine stands, and hence be available to disperse whitebark pine seeds, even at low cone crop densities. Similarly, previous results from the Cascade Range, and Glacier National Park, a location with a relatively low population of Clark's nutcrackers, suggested Clark's nutcrackers used whitebark pine stands with low cone densities [21,22]. Furthermore, Clark's nutcrackers in the Greater Yellowstone did not appear to be abandoning whitebark pine for other habitats in the region. This may be because habitats with alternative food sources were not sufficient for Clark's nutcracker energetic requirements. Limber pine habitat was sparse and patchily distributed, and although the birds foraged on Douglas-fir, they only regularly occurred in Douglas-fir habitat within a habitat mosaic that included whitebark pine. On the other hand, though the Clark's nutcracker-whitebark pine mutualism appears to be functional based on high Clark's nutcracker occurrence in all cone-bearing stands, this high occurrence may not be associated with high levels of whitebark pine seed dispersal. Variability in occurrence could be necessary to ensure cones are not depleted before they have a chance to mature, and before individual Clark's nutcrackers can cache a surplus of seeds, beyond what they need for their energetic requirements.

However, managing for a high cone density to increase the potential of saturating the habitat may not be an effective management strategy. Due to widespread declines in populations of five-needle pines [46], higher numbers of Clark's nutcrackers may regularly move between ecosystems in search of food, oversaturating stands at all cone crop densities. Clark's nutcrackers are facultative migrants, and have evolved to regularly move over the larger landscape, tracking food resources [44]. However, multiple habitats on which Clark's nutcrackers depend are rapidly declining, including whitebark, limber, southwestern white (*Pinus strobiformis*), and pinyon pine (*Pinus edulis*) habitats [7,47–49]. Oversaturation from an increasingly mobile Clark's nutcracker population would lead to areas being "cleaned out" more quickly, and the birds would act as seed predators rather than dispersers a greater proportion of the time.

Though there could be a lag before population numbers change, a lower availability of cones could lead to a decline in the Clark's nutcracker population, and a concomitant breakdown of the Clark's nutcracker-whitebark pine mutualism. A breakdown of the Clark's nutcracker-whitebark pine mutualism would have severe ecosystem-wide consequences. Clark's nutcrackers are a keystone species in western North America, where they play an important role in forest regeneration and seed dispersal for at least ten conifer species [See 6]. Reduced Clark's nutcracker populations would lower the prevalence of their seed dispersal services, and reduce conifer population recruitment. Additionally, without Clark's nutcrackers, whitebark pine regeneration would stop [9]. Numerous species forage on whitebark pine's high-fat, high-energy seeds, and the trees protect watersheds by delaying snowmelt, which leads to decreases in both spring flooding and summer droughts [7,50].

The complication with suggesting management recommendations based on these results, and results from the few previous studies of Clark's nutcracker occurrence patterns, is that the

studies only describe the relationship between Clark's nutcracker and habitat at a snapshot in time [11,12,21,22]. Historical habitat use is unknown. Therefore, we do not know if what we observed is representative of the past, before large-scale declines of whitebark pine and other conifer habitats, or at varying Clark's nutcracker population sizes. Population size, individual fitness and behaviors, including habitat use and selection, can all vary with density of the species and habitats involved in interactions [51,52]. If the local Clark's nutcracker or whitebark pine populations are higher or lower, how does the relationship change?

Predictions of thresholds necessary for continued Clark's nutcracker-whitebark pine stability are based on current conditions, and may be overly simplistic. To improve long-term management outcomes, we therefore suggest adopting an adaptive management approach [53,54]. We suggest continued monitoring of the relationship between Clark's nutcrackers and whitebark pine as environmental conditions change and management strategies are implemented, so that the predictions can be modified and revised with the new information. Because of the conflicting results between Clark's nutcracker habitat use and habitat selection, we recommend a greater focus on differentiating preference versus prevalence. Once habitat availability or Clark's nutcracker population numbers change, how will the birds' behavior change? Due to the high mobility of Clark's nutcrackers and the large-scale declines of many of their habitats, we also suggest monitoring Clark's nutcracker habitat associations range-wide. An increased focus on the status of the Clark's nutcracker metapopulation will allow more robust predictions of stability of the Clark's nutcracker-whitebark pine mutualism.

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Schaming's advisor was the P.I.

Schaming conceived and designed the study, and performed the study. Schaming and Sutherland analyzed the data and wrote the paper.

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CHAPTER 5

RESILIENCE AND FLEXIBILITY OF THE CLARK'S NUTCRACKER-WHITEBARK PINE KEYSTONE MUTUALISM IN A DISTURBED ECOSYSTEM: IMPLICATIONS FOR CONSERVATION OF MUTUALISMS

Abstract

In the face of widespread environmental change, understanding the spatial and temporal dynamics of mutualistic interactions is key to resilience of mutualisms, and in turn, fundamental to designing suitable conservation strategies. To assess stability of the mutualism between Clark's nutcrackers (*Nucifraga columbiana*) and whitebark pine (*Pinus albicaulis*), in this chapter, I examine how Clark's nutcracker habitat use, habitat selection, reproductive success, and dispersal behavior are associated with habitat within the Greater Yellowstone Ecosystem. I discuss how these results influence management strategies for the Clark's nutcracker-whitebark pine mutualism, and consider whether it is effective to concentrate management efforts at the local scale. Additionally, I outline future research questions we need to answer to properly manage this keystone mutualism. Results suggest that whitebark pine conservation strategies need to focus efforts on an ecosystem level, rather than on individual stands. Furthermore, because of their high mobility, resource tracking, and the high proportion of emigrants in my study population, I suggest managers should consider focusing on promoting stability of the Clark's nutcracker metapopulation, rather than managing individual populations. Because Clark's nutcracker habitat associations differed between habitat use and habitat selection, it is critical to discriminate between prevalence and preference when considering the birds' habitat

requirements. I specifically suggest both habitat use and selection need to be monitored throughout the Clark's nutcracker range, to understand how they vary with population abundance, habitat type and quality. Additionally, because long-term survival and reproductive success of the partners, not just short-term continuation of interactions, is critical to mutualism stability, detailed information on the demography and life history of Clark's nutcrackers is also critical to management. The ecological triggers of population-wide nonbreeding and emigration need to be further assessed, so the information can be used to define thresholds of whitebark pine restoration, and be included in estimates of both population viability and probability of seed dispersal. Plasticity of Clark's nutcracker nesting behavior in degraded habitats should also be assessed, so the potential of degraded whitebark pine habitats as an evolutionary trap can be evaluated. In addition, coupling conservation of adjacent alternate habitats with restoration of five-needled pines is a strategy of fundamental importance to Clark's nutcrackers. The Clark's nutcracker-whitebark pine mutualism appeared functional in the Greater Yellowstone Ecosystem, but it is unclear whether the mutualism is stable. To promote conditions that increase whitebark pine regeneration, it is critical to better understand how local Clark's nutcracker occurrence, abundance, and behavior are associated with whitebark pine habitat when cones are both immature and mature, and how changes in Clark's nutcracker demography and behavior alter whitebark pine seed dispersal, germination, and seedling survival. New perspectives on research and management are needed to maintain the integrity of plant-animal seed disperser mutualistic relationships. For effective conservation, I suggest it is critical to assess seed dispersers' population status and behavioral plasticity at the appropriate scale, in relation to all of the habitats on which they depend, and under variable and changing environmental conditions.

Introduction

Maintaining and restoring the integrity of mutualistic interactions is pivotal to effective conservation of biological communities [1,2]. All species are directly involved in one or more, sometimes hundreds of mutualistic relationships [3]. Many mutualisms have persisted and remained stable for thousands to millions of years, but numerous others have shifted and dissolved [4]. Current anthropogenic disturbances are now subjecting many mutualisms to rapidly changing environmental conditions, and it is unclear how resilient and flexible the relationships will be [1].

In particular, worldwide declines in animal seed dispersers have increased the importance of understanding the ecological and evolutionary mechanisms underlying plant-animal disperser mutualisms [5,6]. Animal seed dispersers are critical to healthy ecosystem function in many communities because they enable successful regeneration of seeds, increase regeneration through directed dispersal, alter spatial recruitment patterns, increase gene flow among plant populations, and modify diversity and dynamics of plant communities [See 7]. These seed dispersers enhance ecosystem and species resilience in the face of habitat change by enabling colonization and regeneration of plants in deforested, remote, and disturbed habitats [8–10]. Additionally, a major source of resilience for many plant-animal disperser mutualisms is resource tracking by mobile dispersers, including seed dispersers tracking cone crops, frugivores tracking fruiting trees, and pollinators tracking flowers [11,12]. However, habitat loss often isolates suitable food patches, which constrains resource tracking behavior and leads to lowered fitness of animal dispersers and interruption of seed dispersal [13]. In addition, habitat decline can cause declines of disperser populations, leading to reduced seed dispersal and recruitment [14].

Disruption of mutualistic interactions by habitat loss and degradation can result in a

breakdown of the interactions through mutualism abandonment, or the mutualism shifting to an antagonistic interaction [1,4,15]. Recent research suggests that habitat decline has triggered mutualism breakdown between plants and seed dispersing dung beetles, birds and rodents [14,16,17]. Such mutualism disruptions can have severe repercussions because plant-animal mutualisms are usually highly asymmetric [18–20]. Obligate and near-obligate mutualists typically depend on a generalist [18–21]. The problem is: if a mutualism is asymmetric, and at least one mutualist is facultative rather than obligate, natural selection should favor individuals abandoning the mutualism when costs of continuing to interact exceed benefits gained from the interaction [1]. Furthermore, an obligate mutualist depends on its partner, and will likely be pushed to extinction if abandoned [22].

Current climate change and large-scale habitat decline may be disrupting the health of plant-animal disperser mutualisms because so many interactions within ecological communities are being affected. It is therefore critical to consider whether it is adequate to monitor, protect and manage plant-animal seed disperser mutualisms at the local scale. Focusing on protecting and managing the stability of a single species or pair of species at a local scale can obscure the more important instabilities affecting the populations of one or both of the mutualistic partners over larger geographic scales. In particular, local management of highly mobile animal seed dispersers that track resources over a broad geographic scale may be ineffective if the population is strongly affected by instabilities elsewhere. These mobile species can move out of declining habitats in the short-term, but in the face of large-scale environmental change, may not have adequate habitat on the landscape to support long-term survival and reproduction. Additionally, stability of the interactions with alternative partners of both species in a mutualism need to be considered. What are the alternative partners of each species? Are those relationships stable?

Should those relationships be monitored, protected and managed at a local or broader geographic scale? Finally, strength of mutualistic interactions often vary under fluctuating environmental conditions. Are the conditions changing, and if so, how will these changes destabilize the mutualism? In the face of widespread environmental change, an understanding of the spatial and temporal dynamics of mutualistic interactions is key to assessing resilience and flexibility of mutualisms, and in turn vital to developing suitable management strategies.

In this chapter, I explore our understanding of the resilience and flexibility of the mutualism between Clark's nutcrackers (*Nucifraga columbiana*) and whitebark pine (*Pinus albicaulis*) in the face of large-scale habitat loss. I examine how Clark's nutcracker habitat use, habitat selection, reproductive success, and dispersal behavior are associated with habitat at a local scale, within the Greater Yellowstone Ecosystem. I discuss how these results influence management strategies of the Clark's nutcracker-whitebark pine mutualism, and consider whether it is effective to concentrate management efforts at the local scale. Finally, I outline future research questions we need to answer to effectively manage this keystone mutualism. This synthesis not only has immediate management implications for Clark's nutcrackers and whitebark pine, but also increases our understanding of how to better conserve plant-animal seed disperser mutualisms.

Study system background: Clark's nutcrackers and whitebark pine

Clark's nutcrackers are a keystone species in western North America, where they play a pivotal role in forest regeneration and seed dispersal for at least ten conifer species [See 23]. Whitebark pine is an obligate mutualist of the Clark's nutcracker because it depends on the bird for dispersal of its large, wingless seeds [24–26]. Whitebark pines are declining range-wide due to the combined impacts of *Cronartium ribicola* infections, which cause white pine blister rust, a

mountain pine beetle (*Dendroctonus ponderosae*) outbreak, and long-term fire suppression [27,28]. Even in the Greater Yellowstone Ecosystem, one of the healthiest remaining whitebark pine ecosystems, 46% of the whitebark pine stands are classified as "high mortality" [29]. Clark's nutcracker populations are apparently declining in response to the loss of whitebark and other five-needled pines [28,30,31]. Decreasing populations of Clark's nutcrackers would accelerate the decline of whitebark pines, and this positive feedback loop could lead to mutualism breakdown (see Chapter 4).

Clark's nutcrackers and whitebark pine are considered to be in a keystone mutualism because the Clark's nutcrackers' dispersal of whitebark pine seeds is critical for establishment of unique forest ecosystems [32,33]. Whitebark pine is a keystone and foundational species because it provides high-fat, high-energy nuts for wildlife, facilitates ecosystem succession, and protects watersheds by delaying snowmelt and preventing erosion [33–35]. Clark's nutcrackers move the whitebark pine seeds over long distances, up and down in elevation, and into disturbed habitats [24,33,36]. A breakdown of the Clark's nutcracker-whitebark pine mutualism would have severe ecosystem-wide consequences due to reduced dispersal of conifer seeds by the Clark's nutcracker, and the loss of whitebark pine's important ecosystem functions [32,33]. In addition, the 'keystone mutualist hypothesis' predicts that breakdown of keystone mutualisms can trigger a cascade of linked extinctions [37]. Such cascades are particularly likely in landscapes with degraded native vegetation and when keystone species are lost [38], such as in declining whitebark pine communities.

Protecting and managing Clark's nutcrackers presents a complex conservation challenge. Reliable information on Clark's nutcracker population status, behavioral plasticity and life history is lacking. Because Clark's nutcracker populations are apparently declining due to the

degradation of critical conifer habitats [28,30,31,39], this information is urgently needed. However, Clark's nutcrackers are difficult to study and survey due to a broad range of behavioral, biological and social characteristics [39,40]. The birds have large home ranges, residents leave their home ranges in the fall to harvest seeds from distant sources, and they are facultative migrants that range widely when low to moderate food sources are available [39,41–43]. Because they are both highly mobile and social foragers that readily congregate in areas of high cone production, presence and abundance of Clark's nutcrackers at a location is linked to conifer cone crops [39]. Therefore, changes in year to year variability of occupancy and abundance is a better measure of food availability than of population trends [44]. In addition, Clark's nutcracker detection rates are low and variable, in part because they are not territorial, and like many corvids they do not dependably advertise their presence with songs, calls or displays [40]. Also, many populations occupy remote, subalpine terrain that is logistically difficult to reach, and the breeding season begins as early as January, when there are typically winter conditions [39,45]. For effective conservation of Clark's nutcrackers, their important seed dispersal function, and the Clark's nutcracker-whitebark pine mutualism, it is critical to better assess the birds' population status and behavioral plasticity at the appropriate scale, in relation to all of the habitats on which individuals depend, and under variable and changing environmental conditions.

Behavior and demography

Habitat use and selection

Occurrence patterns

To begin to evaluate stability and resilience of the Clark's nutcracker-whitebark pine mutualism, a first step was to focus on understanding the behavior and demography of a Clark's

nutcracker population within an ecosystem undergoing whitebark pine decline. Between 2009 and 2013, to reveal which resources were important drivers of Clark's nutcracker occurrence and distribution, I evaluated habitat use in the southern Greater Yellowstone Ecosystem, a relatively large region covering approximately 25,000 km^2 (see Chapter 4). I quantified associations between occurrence patterns and habitat to determine which factors impacted the birds' continued use of whitebark pine habitats, and hence their availability to disperse seeds. I focused on evaluating which scale of whitebark pine habitat the birds responded to – cone presence or density, local presence or abundance of the pines, or landscape scale abundance of the pines (within a 32.6 km radius; see Chapter 4). Additionally, I assessed whether Clark's nutcrackers were abandoning whitebark pine for Douglas-fir habitat (*Pseudotsuga menziesii*), the primary local alternative seed source. To understand how the birds were using different habitats, I also conducted behavioral observations of radio-tagged individuals [43,46].

Although whitebark pine in the ecosystem was undergoing severe declines, the birds continued to use whitebark pine habitat, and regularly harvested and cached whitebark pine cones. Clark's nutcracker occurrence was most strongly associated with both the presence of cone-bearing whitebark pine trees and the abundance of whitebark pine on the landscape (see Chapter 4). Mere presence of the birds does not translate into seed dispersal, but presence does mean that the birds were available to disperse seeds. As long as seeds were present, there was a high probability of Clark's nutcracker occurrence, even at low cone crop densities and in high mortality whitebark pine stands. This means that the birds were available to disperse seeds in locations with few cones and poor health. Furthermore, it was feasible to detect evidence of Clark's nutcracker seed harvest in a stand without surveying birds, based on observations of the distinctive "dished out" harvesting scars on the cones [47]. Even in stands with few cones, I

regularly observed "dished out" harvesting scars, suggesting that the birds harvested cones in stands at all cone crop densities. Moreover, not only were Clark's nutcrackers present, but I regularly observed the birds harvesting and caching whitebark pine seeds in stands with varying cone crop densities, and observed Clark's nutcrackers filling their sublingual pouches in whitebark pine stands until all cones were depleted. Because the birds were influenced by landscape abundance of whitebark pine habitat and were highly likely to occur at all cone densities, these observations suggest that conservation strategies need to focus efforts on an ecosystem level, rather than on cone densities in individual stands (see Chapter 4).

Clark's nutcrackers were not abandoning whitebark pine habitats for alternative habitats in the Greater Yellowstone Ecosystem. In fact, unlike other regions [24,48], Clark's nutcrackers in my study area did not move out of the whitebark pine habitats once the whitebark pine cone crop was depleted (see Chapter 4). Instead, I observed the birds using whitebark pine habitats year-round. Additionally, although the birds used Douglas-fir habitat, which provided an alternate seed source, Douglas-fir was primarily used when in a habitat mosaic with whitebark pine (see Chapter 4). Interestingly, after the whitebark pine cone crop was depleted, low Clark's nutcracker occurrence was only likely at locations with a low abundance of both whitebark pine and Douglas-fir habitat, and high Clark's nutcracker occurrence was associated with both a moderate to high abundance of whitebark pine and a moderate abundance of Douglas-fir. On the other hand, probability of occupancy decreased with landscape scale abundance of Douglas-fir during the breeding season, based on abundance within 3.2 km, the average median length of a Clark's nutcracker's home range. These results indicate that there was temporal variation in habitat use, and suggest that Douglas-fir alone was not adequate habitat for Clark's nutcrackers.

A habitat mosaic with both whitebark pine and Douglas-fir habitat appeared optimal, and

I suggest that not only should whitebark pine habitat be managed at a landscape scale, it should be managed within a habitat mosaic with Douglas-fir in the southern Greater Yellowstone Ecosystem (see Chapter 4). Similarly, to increase persistence of Clark's nutcracker populations in a region undergoing whitebark pine restoration, Lorenz [42] proposed managing for healthy ponderosa pine stands in the Cascade Range. By extrapolation, whitebark pine restoration efforts in other regions could be enhanced by restoring whitebark pine stands adjacent to alternative seed sources [43]. On the other hand, proximity to secondary seed resources may not be adequate – the proportions of different conifer habitats in the mosaic are important. Results suggest that in the southern Greater Yellowstone Ecosystem, either too little or too much Douglas-fir on the landscape was negatively associated with Clark's nutcracker occurrence, and Douglas-fir only had a positive association with occurrence where there was a high enough abundance of whitebark pine (see Chapter 4).

Home range size

Knowing the size of an animal's home range helps ensure management is carried out at the appropriate scale. There is only one previous robust estimate of Clark's nutcracker annual home range size, 1,274 ± 1,669 ha (n = 20) in the Cascade Range, Washington [42], and it is unclear if the estimate is representative of home range sizes in all regions. To determine the size of the Clark's nutcracker home range in the Greater Yellowstone Ecosystem, I radio- and satellite-tracked Clark's nutcrackers. First, I radio-tracked 76 adults between 2010 and 2012 [43,46]. I quantified the breeding season home range (March 5 – June 15) [43], as well as the entire pre-seed harvest season home range (January 28 – August 8, 2011 and January 15 – July 29, 2012; Schaming unpublished results). Clark's nutcrackers were not territorial and the ranges overlapped considerably, suggesting that individuals were not excluded from high quality ranges

due to territoriality [43]. During the breeding season, the radio-tagged Clark's nutcrackers had large home ranges, averaging 100 ± 23 for breeding birds in 2012 (n = 27), and 214 ± 53 and 202 ± 53 ha for nonbreeding birds in 2011 (n = 25) and 2012 (n = 3), respectively [43]. Over the entire preharvest season, the radio-tagged birds' home ranges averaged 195 ± 27 ha (n = 56, range = 32 – 1,131 ha; Schaming unpublished results). Preharvest season home ranges of breeding birds averaged 51 ± 18 ha larger than the breeding season home range, whereas nonbreeding birds' home ranges increased by an average of 34 ± 23 ha. Once the birds began harvesting and caching mature whitebark pine seeds, individuals regularly flew back and forth from their preharvest home range to further locations, returning multiple times during the day. During this time, it was often not feasible to home in on or triangulate the bird's location. Therefore, I consider the annual home range sizes of radio-tagged birds to be a minimum area. The average minimum annual home range size increased to 337 ± 58 ha (n = 35), suggesting Clark's nutcrackers in the region require extensive habitat to fulfill their foraging needs.

The area used by the radio-tagged Clark's nutcrackers was relatively large; however, 3 – 10 months (October 2014, postharvest – July 2015, late summer) of satellite-tracking data for seven birds suggests that the radio-tracking vastly underestimated the size of the home ranges outside of the harvest season (Schaming unpublished results). All seven satellite-tagged birds stayed within the Greater Yellowstone Ecosystem, and the home ranges averaged 17,440 ± 4,098 ha, showing that the birds regularly moved over an enormous area. The birds regularly flew over 10 km into multiple different habitat types, including whitebark pine and Douglas-fir, during all months of the year, including the winter and breeding seasons. Unfortunately, the radio- and satellite-tracking occurred in different years (2011 and 2012 versus 2014 through 2015, respectively), and it is unknown if the behavior of the satellite-tagged birds is representative of

all years. However, satellite-tracking data is less biased because it allows for location data to be collected in locations wherever the bird is, as long as the transmitter's solar panels are adequately charged. Even if the birds only use such an enormous area in some years, the fact that they have such a large home range indicates that Clark's Nutcrackers use a larger abundance of habitat to survive than previously thought. It remains to be seen whether they use such a large area in all years, and in regions with other dominant habitat types or better quality habitat. In any respect, these results suggest that managing Clark's nutcrackers at a relatively large scale of a watershed or mountain range within the southern Greater Yellowstone Ecosystem is likely inadequate.

Habitat selection

Assessing both habitat use and selection allows for an optimal understanding of a species' relationship with habitat, because each illuminates different aspects of the relationship. In particular, assessing both illuminates how prevalence is not equivalent to preference, which should be considered when developing conservation strategies based on only use or selection. Habitat use is not a reflection of choice, and the observed pattern may be driven by external constraints such as competition [49]. On the other hand, habitat selection is the behavioral process by which individuals choose certain habitats to use from those that are available [50,51].

To determine the habitats individuals selected for their home range, and for use within their home range, I evaluated habitat selection of radio- and satellite-tagged Clark's nutcrackers. During the breeding season, and over the entire pre-harvest season, the radio-tagged birds selected disproportionately high areas of Douglas-fir habitat from the available habitat on the landscape (n = 55 and 45, respectively) [Schaming unpublished results, 43]. When selecting habitats within the home ranges, the birds used Douglas-fir in proportion to its availability during the breeding season, but selected disproportionately high amounts of Douglas-fir during the

entire pre-harvest season. These results suggest that, at my study site, Douglas-fir habitat is the most important habitat for Clark's nutcrackers prior to the fall whitebark pine harvest, and reinforce the suggestion that a habitat mosaic that contains Douglas-fir is optimal for the birds.

Despite high selection of Douglas-fir habitat, a habitat mosaic with a low, rather than high abundance of Douglas-fir habitat appears most favorable (see Chapter 4) [43]. Although individuals strongly selected Douglas-fir habitat for their home range during both the breeding and preharvest seasons, and probability of use increased in the postharvest season, probability of Clark's nutcracker occurrence was negatively associated with abundance of Douglas-fir during the breeding season (see Chapter 4). These conflicting results could be a simple result of the fact that Douglas-fir was only one of multiple conifer habitats used, and although it was selected, it only made up approximately a quarter of the habitat within breeding season home ranges. Alternatively, Douglas-fir habitat may have been selected for the home range because Douglas-fir cones were a consistent food supply heavily used during the winter months. The Douglas-fir cone crop was high each year, 2008 –2014, and 68 and 83% of the foraging events January through February were on Douglas-fir cones in 2011 and 2012 (Schaming unpublished results). During the breeding season, the radio-tagged birds continued using the same relative areas, but possibly because they primarily foraged on other foods, they did not select Douglas-fir habitat for use within the home range at that time [43].

In contrast to the 2011 and 2012 radio-tracking results, seven satellite-tagged Clark's nutcrackers did not, on average, select disproportionally high amounts of any particular habitat type for their home range outside of the whitebark pine harvest season, between the postharvest stage in 2014 and the preharvest season 2015 (Schaming unpublished results). The birds remained in the southern Greater Yellowstone Ecosystem during this time, and regularly

returned to locations near where they were trapped. On average, Douglas-fir was only used in proportion to availability, although one bird selected Douglas-fir in a disproportionately high amount. Limber pine habitat was the only other habitat selected in a disproportionately high amount by satellite-tagged individuals (n = 5). In addition, when selecting habitat from within the home range, on average, the birds only selected high mortality whitebark pine in a disproportionately high amount. However, only two of the seven birds positively selected the high mortality whitebark pine habitat, while six positively selected Douglas-fir, reinforcing the suggestion that a whitebark pine-Douglas-fir mosaic is important. Unfortunately, the small sample size and high variability makes the results ambiguous; increased numbers of satellite-tagged Clark's nutcrackers would better illuminate which secondary habitats are selected outside of the whitebark pine harvest season.

Breeding strategies and reproductive success

Population-wide nonbreeding

Integrating behavioral studies with population studies is paramount to evaluating health of plant-animal seed disperser mutualisms. Because assessments of population stability, as well as stability of interactions within communities, are often based on counts and occupancy results, rather than fitness data, mutualisms may appear stable when they are not, particularly at the local level. Only with detailed information on the demography and life history of both partners is it possible to predict the continuation of mutualistic interactions. Mutualisms depend on long-term survival and reproductive success of the partners, not just short-term continuation of interactions.

Long-lived plant mutualists, such as whitebark pine and other five-needled pines, may have evolved to be able to wait out temporary absences of pollinators or seed dispersers [3]. However, there may be a threshold at which it is not possible to wait, as regeneration may be so

low for so long that the population declines below some unknown viability threshold. In addition, rapid, large-scale habitat loss and degradation may lead to such high levels of mortality for the long-lived plants that much higher levels of regeneration than historically common are necessary to maintain the population. Absence or low levels of animal seed dispersal would then have outsized impacts. Their inability to disperse adequate numbers of seeds to maintain high levels of regeneration could lead to irreversible repercussions.

A mutualism may appear stable if survival and reproductive success are not evaluated, yet precipitous declines may follow. In a nutritional mutualism, a relationship in which one partner depends on the other for food, individuals may survive if they have adequate food, but low food resources may result in poor body condition, poor survival, and/or poor reproductive success. In fact, the reproductive success of many facultative migrants and irruptive species such as Clark's nutcrackers, pinyon jays, and crossbills, is closely tied to their food supply, and their primary foods are provided by their mutualist conifer partners [39,44,52]. Continued residency, as well as emigration and immigration could all vary with landscape or patch quality, and habitat quality can therefore influence changes in distribution and population structure of both animal dispersers and dispersed tree species [53,54]. Additionally, although a mutualism may have evolved under fluctuating environmental conditions, poor conditions and more extreme conditions are likely to become increasingly common in degraded habitats. Therefore, an understanding of the strategies individuals adopt under different environmental conditions helps illuminate the future trajectory of the mutualism in declining ecosystems where the frequency of poor years is increasing.

Previous authors have suggested that Clark's nutcrackers may forego breeding in years with low food resources [45,55]. Because nutcrackers primarily feed their young conifer seeds

cached the previous autumn, food availability for breeding is determined before birds lay their eggs [45,56,57]. In this study, I documented population-wide nonbreeding in two of five years [46]. The nonbreeding years followed a low whitebark pine cone crop, suggesting Clark's nutcrackers respond to low cone densities by skipping a breeding year, possibly as a life history strategy for increasing survival and lifetime fitness [46]. Although skipping breeding can be an adaptive strategy to maximize lifetime reproductive success, poor environmental conditions can accelerate the rate at which skipping occurs, leading to reduced reproduction and, ultimately, population declines. Several conifers on which Clark's nutcrackers depend are declining [28,58–60], which translates into a higher probability of encountering poor resource years in many preferred habitats. Entire ecosystems that historically provided adequate food may provide insufficient food over enough years that population-wide breeding failure becomes common over a large part of the species' range, and the metapopulation declines. Because Clark's nutcrackers are highly mobile, long-lived, and poorly sampled, there could be a lag in detecting metapopulation declines. In fact, metapopulation decline in response to habitat loss is suggested to incur an "extinction debt" [61]. Determining frequency of years with population-wide nonbreeding in different habitat types of varying quality would allow better predictions of population stability.

Clark's nutcrackers may decline or become locally extinct, then, providing they survive elsewhere, they could recolonize an area once habitat quality improves [43]. Given the widespread decline of five-needle pines, however, ensuring a persistent, stable population of Clark's nutcrackers in an ecosystem may be the best management practice, because it would ensure Clark's nutcrackers are always available to cache seeds. Additionally, Clark's nutcracker seed caching enables conifer regeneration, and this seed dispersal ecosystem service itself is an

efficient conservation tool, which provides a cost-effective alternative to human labor [62]. Near extinction of a local corvid population has been shown to severely limit regeneration and spatial spread of large-seeded plants [63].

A better understanding of the ecological thresholds that trigger Clark's nutcrackers to breed versus skip breeding, and determining whether there is an increased frequency of the triggers or conditions that lead to nonbreeding, would aid development of conservation strategies. In several species, nonbreeding is triggered by a threshold of food abundance [64,65,See 66]. I found that population-wide nonbreeding occurred in years with an average cone crop ≤ 8 cones per tree ($n = 2$), and breeding occurred in years with ≥ 20 cones per tree ($n = 3$) [46]. First, quantifying likelihood of nonbreeding over multiple years would allow greater confidence in the association between cone crop and nonbreeding. Then, by determining how the number of cones per tree translates into the number of cones per ha, then evaluating the specific cones per ha threshold above which breeding occurs, managers could attempt to restore enough whitebark pine on the landscape that adequate numbers of seeds are available for breeding to occur in all but the lowest mast years.

Whitebark pine habitats are rapidly disappearing, and fewer trees likely translates into fewer cones, even in high mast years. If individual Clark's nutcrackers stay in whitebark pine ecosystems and skip breeding in an increasing number of years, their lifetime reproductive success would decline, and individuals may be caught in an evolutionary trap, a situation in which rapid environmental change renders the behavioral decisions individuals make maladaptive [67]. Even if it is not feasible to alter conditions to an extent that the number of breeding years increases, knowing how often nonbreeding occurs is critical to accurately estimating Clark's nutcracker population viability in ecosystems.

Fledging success

Habitat loss can adversely affect avian reproductive success by lowering nestling survival [68,69]. In 2012, I evaluated the association between probability of fledging young, and habitat at the landscape, local and nest site scales (n = 29; Schaming unpublished results). I defined the landscape as 101 ha, the average size of a Clark's nutcracker breeding season home range [43], the local scale as the habitat measured by the modified point quarter technique (≤200 m), and nest site as within 50 m. Only three habitat variables strongly influenced fledging (Schaming unpublished results). Reproductive success increased with increasing abundance of whitebark pine on the landscape. In contrast, reproductive success decreased with both increasing dominance of dead whitebark pine at the nest site, and increasing abundance of Douglas-fir on the landscape. These results suggest that, to increase probability of fledgling success, Clark's nutcrackers in the study area should prefer a home range that includes more whitebark pine and less Douglas-fir habitat. However, the majority of the whitebark pine stands in the study area were experiencing moderate to high or high mortality [29]. Therefore, the strong negative effect of high levels of whitebark pine mortality at the nest site could counteract the benefit of nesting in a landscape with abundant whitebark pine. It is unknown if the negative impacts of whitebark pine mortality on reproductive success lead to individuals altering their nesting behavior, or if birds will make maladaptive decisions and continue to nest in high mortality stands, leading to an evolutionary trap. Examining whether Clark's nutcrackers with failed nests renest in locations with higher quality habitat, within both the same year and subsequent years, would allow assessment of the potential occurrence of an evolutionary trap. If data suggests a trap is occurring, it would be important to take this into account when estimating Clark's nutcracker population viability.

Clark's nutcracker dispersal behavior

Habitat degradation can affect the frequency of emigration to a point where birds are leaving ecosystems more frequently to search for higher quality habitats that have become far less abundant. An environmental threshold that triggers dispersal may have been adaptive under historical conditions, but could become a liability in the face of large-scale habitat decline. Many seed dispersers and pollinators, which regularly move throughout a region to track resources, are particularly vulnerable to extinction because they depend on large tracts of forests in widely separated areas [70]. Moreover, as occurred with Newfoundland crossbills (*Loxia curvirostra percna*) and passenger pigeons (*Ectopistes migratorius*), because of their movements, large declines of mobile seed dispersers may go undetected [71,72]. Research suggests that habitat loss, fragmentation, and degradation has led to large declines in populations of previously common, high mobility habitat specialists [73].

Clark's nutcrackers have evolved to regularly move over the larger landscape to track food resources [41,74]. In the face of habitat loss and degradation, these long-distance movements can mitigate effects of decreasing patch quality because the birds can easily move to higher quality habitats [75]. However, because several conifer habitats that provide Clark's nutcracker food resources are declining [28,58–60], birds that disperse may continue roving in search of adequate habitat, or settle in poorer quality sites with reduced survival and reproduction.

Previous research suggested that individual Clark's nutcrackers will disperse at varying levels of food abundance [41]. In years with moderate or low seed production, "emigrants" would range regionally and forage opportunistically in the fall, whereas "residents" would remain in stable home ranges during all but the lowest cone crops [41]. It is unclear what the

specific ecological triggers and thresholds are that drive individuals to emigrate. Behavioral studies are needed to determine how Clark's nutcrackers assess habitat, specifically, whether they do so based on food intake rates, seed encounter rates, or some other mechanism. Additionally, it is unknown how long emigrant Clark's nutcrackers rove before settling, how far individuals will travel, and whether emigrants depend on cached seeds for overwinter survival. Finally, it is unknown if the frequency of emigration is increasing due to declining habitat, and if so, if there is a fitness cost that would impact health of the metapopulation.

Understanding the rate of emigration during varying cone crop densities, and the scale over which Clark's nutcrackers regularly move can help managers both evaluate population viability in a region, and determine the scale at which to focus their efforts. In my study, 7 – 71% of the tagged Clark's nutcrackers disappeared from the study area in each of the three years of systematic radio- and satellite-tracking (Schaming unpublished results). Disappearance of a radio-tagged Clark's nutcracker may have resulted from the bird dying, losing its antenna, permanently dispersing, or temporarily emigrating (not returning to the study area (~1,220 km^2) until after the field season ended, November 20, 2011 or October 31, 2012) [46]. However, based on the satellite tracking data, I have solid evidence that at least a portion of the birds that disappeared moved out of the study area near Jackson, Wyoming, and settled in a different region (Schaming unpublished results). One satellite-tagged bird flew to Montana where it was last located in early November, so its overwintering location was unknown. Four flew to Utah, up to 650 km away, where they settled, overwintered and continue to reside (as of May 17, 2016). The behavior of the satellite-tagged Clark's nutcrackers suggests that at least a portion of the missing radio-tagged birds also temporarily or permanently moved out of the study area.

Counter to the prediction that movement is initiated due to low food supplies [41,74], a

high proportion of tagged individuals (71%, n = 24) disappeared from the study area in 2012, a fall with a high cone crop. Then, in 2015, the majority of the satellite-tagged birds (71%, n = 5) emigrated during a moderate whitebark pine cone crop. This suggests that higher cone crops in the Greater Yellowstone may now be perceived by Clark's nutcrackers as lower due to the presence of fewer whitebark pine trees. Even if remaining live trees have high numbers of cones, fewer trees would lead to fewer cones available during both high and low mast years. These fewer cones could mean that the habitat is more frequently below some critical cone crop threshold at which higher numbers of individuals emigrate. If a high cone crop in the Greater Yellowstone is insufficient for retention of a majority of Clark's nutcrackers, the birds may move out of the ecosystem more frequently than previously suggested. It is unknown if these high rates of emigration were common historically, or if the decline of whitebark pines and other food resources have led to increases in frequency of these long distance movements. Satellite-tracking Clark's nutcrackers trapped in multiple ecosystems would allow assessment of the proportion of emigrants and residents in each region, as well as their rates of emigration and colonization. In addition, satellite-tracking could be used to evaluate movement between ecosystems in years with different levels of cone crops. These data would enable an understanding of how Clark's nutcrackers track resources, including how far they fly, how long they stay in patches of different quality, and the costs of movement in terms of survival.

Previous research has shown that Clark's nutcrackers rapidly switch food sources within an ecosystem based on rates of energy gain [48]. Satellite-tagged birds moved from whitebark pine habitat to pinyon pine habitats in Utah, suggesting Clark's nutcrackers will readily abandon whitebark pine ecosystems for other conifer ecosystems, and local population rates could rapidly fluctuate in a region (Schaming unpublished results). Additionally, each year, I observed the

majority of tagged emigrants leaving the study area after the fall harvest season began, suggesting that the habitat was oversaturated by the birds. If oversaturated, fewer whitebark pine seeds would survive until maturity, and seeds would be depleted sooner in the fall, resulting in a shorter harvest season. A shorter harvest season could translate into fewer seeds cached per bird, and a higher proportion of seeds retrieved per bird, hence fewer regenerating whitebark pines. In the absence of the ability to swamp predators, whitebark pines could become functionally extinct due to lack of dispersal and regeneration [76,77]. Assessing the relationship between local Clark's nutcracker abundance, cone density when cones are both immature then mature, and the level of germinating whitebark pine seedlings would allow a better understanding of the conditions that increase whitebark pine regeneration.

Finally, one of the most important ecosystem services of Clark's nutcrackers is their long-distance seed dispersal. The problem is that even though they are moving farther, a greater proportion of emigrants would effectively reduce seed dispersal distance. Emigrants tend to cache seeds closer to harvest stands than residents, up to 1.7 versus 32.6 m away [23,36]. Additionally, emigrants are suggested to forage primarily on germinating whitebark pine seedlings in the summer, and loss of seedlings would likely reduce regeneration. On the other hand, because emigrants leave an area before retrieving their seed caches, their impact on seedlings may be counter-balanced by their failure to eat most of their cached seeds. Although logistically difficult, a better understanding of differences in seed dispersal and foraging behaviors between emigrants and residents would be particularly important for management strategies in regions where Clark's nutcrackers are unlikely to occur outside of the fall harvest season, and therefore all individuals are emigrants, merely moving through the area.

Broad considerations for management of the Clark's nutcracker-whitebark pine mutualism

It is unclear whether the Clark's nutcracker-whitebark pine mutualism is stable in the Greater Yellowstone Ecosystem. However, because the birds were likely to occur in stands at all cone crop densities regardless of whitebark pine health, and I observed the birds harvesting and caching seeds throughout the harvest season, the mutualism appeared functional in the study area. Conducting population viability analyses for the birds and trees, evaluating survival and reproductive success of each, as well as Clark's nutcracker immigration and emigration levels, would be necessary to determine stability of the populations, which is key to assessing stability of the mutualism.

A complication with basing management recommendations on our current state of knowledge of Clark's nutcracker-habitat associations is that both previous studies and my research only evaluate the associations at a snapshot in time, and at a small spatial scale relative to the Clark's nutcracker range. What I observed may not be representative of the past, before large-scale declines of whitebark pine and other conifer habitats in the western U.S. Additionally, by studying both Clark's nutcracker behavioral and population ecology in concert, I recognized that habitat use and habitat selection were dissimilar, suggesting that it is critical to differentiate between prevalence and preference when assessing the importance of different habitats, and management strategies based on just habitat use or selection could lead to ineffective results.

Behaviors, including habitat use and selection, as well as population size and individual fitness, often vary with density of species and habitats [e.g. 78,79]. Once habitat availability or

Clark's nutcracker population numbers change, the birds' habitat use and selection could vary. Clark's nutcrackers could respond differently to whitebark pine cone presence and density in locations experiencing different levels of habitat decline. Abundance of Clark's nutcrackers in the region could alter the birds' response to habitat type or quality. Of particular conservation importance, in locations with few Clark's nutcrackers and heavily degraded habitat, birds could respond differently as compared to their behavior in better quality habitat. What factors increase the potential of a weakening or breakdown in the mutualism? How can we promote mutualism stability and resilience? To improve long-term management outcomes, adopting an adaptive management approach, and continuing to assess the relationship between Clark's nutcrackers and whitebark pine is critical as environmental conditions change and management strategies are implemented (see Chapter 4) [80,81].

At what scale do we need to monitor and manage Clark's nutcrackers?

Due to the high mobility of Clark's nutcrackers, and the large-scale declines of many of their habitats [e.g. 33,41], range-wide research and management is necessary. Large-scale assessment, even though it would at first be a snapshot in time, could allow us to begin to answer critical questions about how Clark's nutcracker demography, behavior, and their important seed dispersal function, varies with habitat type and tree health. Local information on Clark's nutcracker demography as it relates to patterns of movement and habitats occupied, would provide information needed to prioritize restoration efforts, such as location and size of restoration sites. Continued tracking to examine how behavior changes with varying population abundance, habitat types and health would help to predict between-patch movement, and the costs of moving, as well as fitness of emigrants versus residents in ecosystems of various quality.

With these results, we should be able to predict if the birds will be available to continue their important seed dispersal function in regions where they are currently abundant, as well as in regions with lower populations, such as Glacier National Park [31,47].

It is undeniably a challenge to monitor and manage at the spatial scale of the metapopulation. However, an effective approach to conservation of many plant-animal seed disperser mutualisms, especially those that involve resource tracking by nomadic species or facultative migrants, such as Clark's nutcrackers, is to focus on the stability of the metapopulation, rather than concentrating on protecting one or few populations or locations. After all, for highly mobile species, successful conservation at one site often depends on conditions at other sites that can be geographically distant [82]. Severe threats to the stability of a mutualism might not be perceived at the local scale, and a decline of commonly inhabited regions can portend rapid decline of the metapopulation by creating extinction debt. Although a local Clark's nutcracker population, such as that in the Greater Yellowstone Ecosystem, may appear stable, the population may be artificially high due to annual immigration from other areas. Because so many habitats are declining, there could be high numbers of emigrating birds from other failing ecosystems. Because large numbers of emigrants from other regions can be attracted to cone-producing stands in the fall, they can inflate population size during the fall seed harvest [23,41]. Although immigration could ensure that Clark's nutcrackers are available to disperse seeds, a highly mobile Clark's nutcracker population could instead commonly oversaturate ecosystems at all cone crop levels, something that may have happened only rarely prior to the advent of widespread conifer mortality.

Regular range-wide movements may not reduce fitness of these long-lived birds, but there is presumably a threshold at which the costs and uncertainty of emigration become too

high, whether or not they outweigh the benefits of remaining in a location. If, due to declining habitat, individual Clark's nutcrackers are moving over the larger landscape at higher than historical levels, and these movements lead to even a slight decrease in fitness of a large number of individuals, this could lead to metapopulation decline. An evaluation of the fitness of individuals that adopt a strategy of staying rather than leaving at varying levels of whitebark pine cone crop densities could aid in predicting Clark's nutcracker metapopulation stability.

Finally, as whitebark pine continues to decline, alternative food sources may be increasingly important for supporting local Clark's nutcracker populations and, indeed, they may be fundamental to conservation of whitebark pine, and the mutualism on which whitebark pine depends. Effective conservation strategies likely require protection of a network of key areas that include both primary and potentially important alternate habitats [83]. Secondary habitat needs are regularly overlooked [84], but even habitat-specialist species, such as black-backed woodpeckers (*Picoides arcticus*) and grizzly bears (*Ursus arctos*), often use secondary habitats during different life stages, and under varying environmental conditions [84,85]. Alternate habitats may become refugia when there is a reduction in primary habitat, and may be critical for long-term population viability [85,86]. Coupling conservation of adjacent alternate habitats with restoration of five-needled pines is a strategy of fundamental importance to Clark's nutcrackers.

How do we begin to assess Clark's nutcracker habitat associations and population trends range-wide?

Given the widespread decline of five-needle pines and the distances moved by Clark's nutcrackers, a system-wide conservation strategy is needed. It should be supported by increased research effort to fill in the existing holes in our understanding of the relationship between habitat quality, landscape quality, and Clark's nutcracker seed dispersal. Researchers regularly

use data from citizen science Breeding Bird Surveys, Christmas Bird Counts, FeederWatch and eBird data to determine if bird populations and distributions are stable, increasing or decreasing [e.g. 87–89]. However, because of their behavior and remote location, Clark's nutcrackers are poorly captured by these methods [39,40]. To assess both Clark's nutcracker habitat associations and population trends range-wide, I suggest the need for a focused citizen science project targeting collection of large quantities of data across a broad spatial scale and in numerous habitats over a long time period [90]. Focusing the eBird audience using "extreme citizen science" contests could help garner the data needed to better understand spatial variation in probability of occurrence for this magnificent bird.

Timing of data collection is an important component to consider when collecting data and developing management strategies. Lorenz and Sullivan [40] recommended that local populations should be estimated during July to ensure counts of residents versus emigrants. In the Greater Yellowstone, I observed emigrants leaving the region during the fall, so they would be counted as residents in July. Therefore, I suggest that surveys be conducted during the breeding season to determine if individuals are remaining on the landscape year-round. In addition, I recommend surveys during the late summer, once Clark's nutcrackers are harvesting immature whitebark pine seeds, to determine if the Clark's nutcracker population is so high compared to the cone crop that few seeds will survive to maturity. On the other hand, surveys during the fall harvest may provide the appropriate information for many management decisions. Fall surveys would determine the extent to which Clark's nutcrackers are present and dispersing seeds. Multiple surveys of population size and the cone density, throughout an ecosystem, for the duration of the harvest season, would allow understanding of whether enough seeds are available to meet and exceed Clark's nutcracker's energetic requirements in winter and during the

breeding season. In addition, I suggest that even if the primary interest is on conserving the Clark's nutcracker-whitebark pine mutualism in a local region, such as the Greater Yellowstone Ecosystem, Clark's nutcracker surveys should be conducted across the birds' range because stability of the Clark's nutcracker metapopulation needs to be assessed.

Furthermore, overlaying Clark's nutcracker citizen science survey results, and eBird occurrence maps on habitat maps would allow assessment of the habitat mosaics used by Clark's nutcracker populations throughout the year [91]. Habitat maps are readily available from national forests and parks, the Bureau of Land Management, National Aerial Survey Data, and whitebark pine aerial survey datasets [e.g. 46]. Additionally, satellite imagery could be compared to the habitat maps, to determine whether remotely sensed imagery could be used to delineate habitats in areas without adequate habitat maps, and to enable predictions of changing Clark's nutcracker habitat use in locations where conifers are experiencing ongoing declines.

Conclusions

A breakdown in the Clark's nutcracker-whitebark pine mutualism could expand and accelerate effects of habitat loss and degradation because mutualists are bound to a common fate [1]. Maintaining the Clark's nutcracker seed dispersal function in whitebark pine ecosystems and throughout their range is critical to managing western forests. However, managers of whitebark pine are currently focused nearly exclusively on work in whitebark pine forests, without accounting for the mobility of Clark's nutcracker populations [76,92]. They have focused on restoring whitebark pine habitat, assuming that Clark's nutcrackers will be available to resume seed dispersal once the forests reach an adequate state of health. It is therefore critical that Clark's nutcrackers persist in or move back into locations after whitebark pine habitats are restored [43].

To ensure stability of the Clark's nutcracker-whitebark pine mutualism, I suggest that managers should focus on promoting stability of the Clark's nutcracker metapopulation. First, Clark's nutcracker prevalence and preference needs to be monitored in multiple ecosystems throughout their range to more fully understand the response of Clark's nutcrackers to habitat loss. Second, the ecological triggers of population-wide nonbreeding and emigration need to be further assessed to better understand and ameliorate negative impacts of large-scale habitat loss on the species. Third, for effective conservation of the Clark's nutcracker-whitebark pine mutualism, it is important to recognize that Clark's nutcracker relies on many other habitats and that whitebark pine cannot be managed in isolation. I suggest whitebark pine needs to be protected within a habitat mosaic with other confers on which Clark's nutcrackers forage. In addition, the impact of the health of these alternative food sources should be considered in both local ecosystems and at the scale of the Clark's nutcracker's range. Fourth, to promote conditions that increase whitebark pine regeneration, it is critical to understand the association between local Clark's nutcracker abundance, whitebark pine cone density when cones are both immature and mature, and the abundance of germinating whitebark pine seedlings.

As ecologists have begun to recognize the importance of managing for communities, rather than single species, this work points to the need to consider interactions and the relevant scale of interactions. New perspectives on research and management are needed to maintain the viability and integrity of numerous mutualistic relationships. Impacts of habitat decline on mutualism stability, and in particular, the response of avian seed dispersers to decline of their plant mutualists, are poorly understood [30]. A focus on ensuring the stability of plant-animal seed disperser mutualisms may be particularly important to increase the ability of plants to move into newly disturbed or available habitats. I propose three nonmutually exclusive key

considerations that should be investigated when designing a conservation plan for species involved in strong mutualistic relationships: (1) Evaluate the spatial scale at which a mutualism and mutualistic partners should be protected and managed. To conserve the integrity of a mutualistic interaction at a local scale, it may be critical to focus on maintaining the populations and interactions of each partner at a larger landscape scale. Rather than concentrating on protecting one or few populations or locations, managers may need to focus on enhancing the stability of the metapopulation. (2) Assess alternative mutualistic relationships for each partner, and determine if the health of these alternative interactions is critical to the health of the focal mutualism. (3) Assess variation in the mutualistic interaction under different environmental conditions, and consider the impacts of the trajectory of future environmental change at both population and individual levels. For effective conservation of the Clark's nutcracker-whitebark pine mutualism, as well as other plant-seed disperser mutualisms, it is critical to assess seed dispersers' population status and behavioral plasticity at the appropriate scale, in relation to all of the habitats on which they depend, and under variable and changing environmental conditions.

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